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Errata in Volume XLIV:—

Page 100, caption Fig. 13, read:

Fig. 13. Geographic distribution and origin of genera. Arrows point from the less specialized to the more specialized of the two most closely related taxa, and in one genus and one in the other.

Page 101, caption Fig. 13 (Continued), line 1—For "heavy" read "dotted'.

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Vol. 44 FEBRUARY, 1957 No. 1

SOME LICHENS OF TROPICAL AFRICA. II. USNEA. (*Continued*)

CARROLL W. DODGE*

1. USNEA CERVICORNIS Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Southern Rhodesia, Makoni Inyanga District, summit of Forrest-Hill Kop, 1700 m., on shaded rock face, *Frederick Eyles 827*, at Kew.

Thallus erect, forming fragile tufts up to 8 cm. tall from a common holdfast, root-like fibers more than 2 mm. long (broken); unbranched or irregularly dichotomous, 2 mm. in diameter, terete, somewhat flattened at the axils, citrine drab shading to olive buff above, not articulate nor inflated; surface areolate, subfoveolate, minutely and irregularly papillate, papillae with black tips mostly broken off, leaving white punctiform scars, the younger portions smooth, irregularly white-reticulate; eramulose.

Apothecia lateral, about 1 cm. below the recurved tip of a branch, 8 mm. in diameter, margin crenate, eciliate or with one to two cilia up to 8 mm. long, about 0.5 mm. in diameter, somewhat inflated in the middle, with obtuse tips; disc epruinose, ochraceous salmon or buffy brown; exciple surface similar to that of the thallus but cortex scarcely areolate and less white-punctate. Cortex fastigiate, 40–65 μ thick, of slender hyphae in a gel, the outer 12 μ deeply staining, heavily nubilated with minute brownish crystals, penetrated by occasional filaments of *Trentepohlia,* moniliform, cells nearly isodiametric, 7–8 μ in diameter, outermost spherical protoplast not uniformly staining (cleavage of zoospores?). Medulla about 65 μ thick, thinning somewhat toward the margin, of loosely woven, thick-walled hyphae about 4 μ in diameter, heavily nubilated with minute hyaline crystals; algal layer under the parathecium about 25–30 μ thick; parathecium hyaline, 40 μ thick, hyphae perpendicular to the surface, thick-walled, slender, conglutinate; hypothecium of slender, somewhat loosely woven periclinal hyphae; thecium 75–

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Issued March 14, 1957.

80 μ tall; paraphyses conglutinate, upper 15 μ heavily nubilated with brown crystals, tips not thickened; asci clavate, 40–45 × 10–12 μ, tips thickened when young; ascospores 8, monostichous, unicellular, about 8 × 4 μ (in ascus probably not quite mature).

Cortex of branch 190–200 μ thick, consisting of an outer layer 40 μ thick, of slender, predominantly radial hyphae so heavily nubilated by brown crystals that structure not clear even in thin sections, and a gelified layer 150–160 μ thick, of hyaline, thick-walled, branched and interwoven hyphae predominantly radial; algal layer about 30 μ thick, of radial filaments of *Trentepohlia*, cylindric, 6–8 μ in diameter, cells nearly isodiametric, sending broad columns of filaments up through the cortex, 25–135 μ thick, forming fracture planes for the areolate cortex; medulla 80–95 μ thick, of thick-walled, branched and interwoven hyphae, so densely nubilated with brown crystals that the structure is obscured; axis hollow, stuffed, 1500 μ in diameter, chondroid cylinder shallowly lacerate on the outside, more so within, 250–300 μ thick, of very thick-walled, interwoven, branched, predominantly longitudinal hyphae, lumen about 1 μ in diameter; cavity 500–750 μ in diameter, loosely stuffed with interwoven, predominantly radial hyphae 5–6 μ in diameter, lumen 1–2 μ, growing out as branches from the axis hyphae.

This species is closest to *U. Liechtensteinii*, with a narrower cavity, ramuli and white-tipped papillae; the apothecia are terminal with a rugulose exciple.

2. USNEA PERHISPIDELLA Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:210. 1897.

Type: Kenya, Machakos, *Liechtenstein & Pospischill.*

Thallus about 6 cm. tall, fruticose, rather rigid, pale grayish green, drying raw umber to antique brown in the herbarium; base thick, slightly fuscous, often giving rise to several branches, rather closely dichotomous, internodes mostly 6–8 mm. long, axils acute to nearly right angles; branches about 2 mm. thick below, about 1.2 mm. thick above, continuous or distinctly annularly cracked, cortex subareolate, areoles plane, terete or only slightly deformed; papillae minute, elongating to short spinulose isidia which soon break away leaving minute pseudocyphelliform scars, often confluent in short rows, more rarely germinating *in situ* as slender pseudoramuli 2–3 mm. long, slightly curved upward; ultimate branches flexuous, slender, tips acute.

Apothecia lateral, then appearing subterminal, sessile, 3–5 (–6) mm. in diameter, concave, cup-shaped, finally subplane; exciple rugose with short spines; marginal cilia rare, subdistant, mostly 2 mm. long, conic, a few up to 10 mm. long with spinules at their base; ascospores 10–13 × 7–8.5 μ in clavate asci.

Cortex up to 80 μ thick, dilacerate, chondroid, fragile, of predominantly periclinal hyphae, the outer 20 μ brownish, deeply staining, almost a thick-walled pseudoparenchyma; algal layer 25–50 μ thick, of radial filaments of *Trentepohlia*,

cells 6–7 × 10–11 μ; medulla 180μ thick, closely woven to subarachnoid, K sulfur-yellow; axis solid, about 360 μ thick.

Only two young plants with a single apothecial initial were found in the material from S. Sudan. The material from Kenya is typical.

S. SUDAN: Issore, Onejiro, 1775 m., corticole, 3° 50′ N., 32° 50′ E., *T. F. Chipp 57*, at Kew.

KENYA: Endabarra-Mau Forest, 2355 m., on *Acacia*, *P. R. O. Bally B4947*, in E. African Herb.

3. USNEA SOREDIOSULA Müll. Arg. in Motyka, Lich. Gen. Usnea Stud. Monog. 330. 1937.

Type: Tanganyika, Usambara, near Kumba marsh, *C. Holst* sub *U. barbata* v. *sorediosula* Müll. Arg. at Genève.

Thallus erect, rigid, fruticose, up to 8 cm. tall, pale ashy, drying deep olive buff from soredia, exposed portions of the axes Isabella color; holdfast conic, black, up to 4 mm. in diameter; base cylindric, 3 mm. tall, about 2 mm. in diameter, annularly cracked; repeatedly, often unequally, dichotomous at acute or right angles, the branches 1.6 mm. in diameter below, more slender at each dichotomy, variously curved and intricate, rarely concrescent, forming a dense tangle broader than tall; terete, indistinctly annularly cracked or subareolate below, smooth above between the low tubercles which are rather close, sometimes in rows or rarely concrescent in short low ridges, soon forming isidiose soredia and appearing farinose as the soredia are dispersed over the whole plant, except less dense over the basal internodes; eramulose; summits up to 20 mm. long, subcapillaceous, rather closely dichotomous but mostly broken off. Apothecia not seen.

Cortex up to 160 μ thick, very densely woven in upper 30 μ, more loosely woven below, imbedded in a yellow gel; algal layer up to 130 μ thick, of radial *Trentepohlia* filaments, cells up to 10 μ long, 6–7 μ in diameter, below forming a continuous layer about 50 μ thick with projections into the cortex up to 80 μ tall and some filaments growing in columns to the surface of the cortex to form the soredia; medulla 65–125 μ thick, very densely woven under the algal layer and next the axis, loosely woven between, hyphae 4–5 μ in diameter, lumen 1 μ, nubilated with brownish crystals; axis 430 μ thick, of interwoven hyphae 3 μ in diameter, lumen 1 μ, conglutinate, predominantly longitudinal.

UGANDA: Kigezi, Kabale River, on trees, 1970 m., *I. R. Dale L1*; Mafuga, 2580 m., *I. R. Dale 42*; Ruizi River, 1390 m., *T. Jarrett 402*; all at Kew.

4. USNEA NUTANS Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Kenya, Northern Frontier Province, Mt. Kulal, 1935 m., on exposed rock, *P. R. O. Bally 5685*, at Kew.

Thallus erect to decumbent, rigid especially below, about 8 cm. tall, cinnamon buff on the main axes shading to dark olive buff on the ultimate branches; holdfast black, hemispheric, 5 mm. in diameter, forming root-like structures below, giving

rise to 10 or more primary axes above; bases below the first dichotomy varying from 1 to 10 mm. long, 1.5–2 mm. in diameter, blackened below; branching variable, dichotomous, at nearly right angles, the branches curving upward with short internodes below, then longer internodes and spreading branches in the mid-portion, more closely branched and the branches recurved above, terete, smooth below with the cortex annularly cracked and subareolate, minutely verrucose above, each verruca bearing a single short isidium, black-tipped, decadent, leaving minute white scars; eramulose; the nodding ultimate branches smooth, minutely black-tipped. Apothecia not seen.

Cortex up to 200 μ thick, cartilaginous, outer 40 μ fastigiate, of slender hyphae heavily nubilated with brownish crystals, the rest of loosely woven, branched and anastomosing hyphae in a gel, in some places penetrated by strands of somewhat disorganized algal filaments from below to a height of 100 μ; algal layer variable in thickness, up to 50 μ, of radial branched filaments of *Trentepohlia* 5–6 μ in diameter, somewhat moniliform, cells 7–8 μ long, apparently not helping to form the cortical cracks as in other species of this section; medulla about 100 μ thick, of densely woven, slender hyphae 3 μ in diameter, heavily nubilated with brownish crystals, tending to tear apart in the middle, allowing areoles to flake off and making sectioning difficult; axis 550–575 μ in diameter, the inner half minutely lacerate, forming many small stuffed cavities, not a single cavity as in most other species.

The habit of our species is reminiscent of a tuft of a species of *Cladina* with recurved tips. It resembles the smaller *U. capensis* somewhat in habit but differs in many macroscopic and microscopic details.

UGANDA: Kigezi, Kabale River, 2260 m., on tree, *I. R. Dale L43*, at Kew.
KENYA: Northern Frontier Province, Mt. Kulal, 1935 m., on exposed rock, *P. R. O. Bally 5686*, type at Kew.

5. Usnea Dodomae Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Tanganyika, Dodoma Prov., Mt. Mpwapwa, 1610–1935 m., saxicole, *P. J. Greenway 2432*, in East African Herb.

Thallus erect or decumbent in dense tufts, 10 cm. tall, rigid, from a common holdfast, up to 15 mm. in diameter, of dense yellowish, root-like processes at least 3 mm. long, penetrating between the rock crystals; branches about 1.5 mm. thick at the blackened base, expanding to 2 mm. below the first dichotomy, 10–15 mm. above the holdfast; further branching variable from dichotomous to almost sympodial, ultimate branches up to 7 cm. long; flexuous, tapering gradually to the acute tip; eramulose (occasionally the ultimate branches once or twice unequally dichotomous 1–2 cm. from the tip, forming pseudoramuli), light brownish olive shading upward through Isabella color to almost honey yellow at the tips; not articulate nor inflated; cortex cracked and subareolate below, otherwise smooth, densely covered throughout most of the plant with short spinulose isidia which

soon break away leaving minute punctate scars (appearing as pseudocyphellae or when aggregated in short rows on indistinct ridges, giving a slightly foveolate appearance), the ultimate 2 mm. nude of spinules. Apothecia not seen.

Cortex about 180 μ thick, horny, fastigiate above (upper 15 μ), more loosely woven below, all imbedded in a gel; algal layer about 50 μ thick, of more or less radial filaments of *Trentepohlia* 4–5 μ in diameter, cells varying from isodiametric to 8 μ long; medulla 65–70 μ thick, of very densely woven hyphae, nubilated with brown crystals, thick-walled, easily cracking away from the axis in sectioning; axis about 970 μ in diameter, hollow, the walls about 360 μ thick, of very densely woven, thick-walled hyphae in a gel; central cavity somewhat irregular in outline, 250–350 μ in diameter, stuffed with loosely woven brownish hyphae.

TANGANYIKA: Dodoma Prov., Mt. Mpwapwa, 1619–1935 m., saxicole, *P. J. Greenway 2432*, in E. African Herb.

6. USNEA PULVINULATA Dodge, Ann. Mo. Bot. Gard. 43:392. 1956.

Type: Uganda, Kigezi, Kasatoro forest, 1935–2560 m., on trees, *I. R. Dale L39*, at Kew.

Thallus fruticose, erect, up to 5 cm. tall, between wood brown and deep olive buff (seen from above), the main branches citrine drab, blackening below; holdfast a black verrucose disc about 8 mm. in diameter, the base black, about 4 mm. tall, 2 mm. in diameter; branching dichotomous to sympodial, internodes short, producing a subhemispheric tuft, the ultimate branches about 2 cm. long, 1 mm. in diameter, annularly cracked and subareolate in the lower blackened portion, otherwise smooth but very densely ramulose, the ramuli rather fragile below and the broken bases suggesting papillae, some regenerating as several spinules which probably serve as isidia; the cortex cracking off in patches, exposing the light coral red lower medulla and surface of the axis; ramuli acuminate, 0.5–3 mm. long, straight, axils acute.

Apothecia subterminal, mostly appearing terminal, up to 15 mm. in diameter, cupulate at first, becoming nearly plane; exciple shallowly scrobiculate, closely ramulose along the ridges; marginal cilia crowded, about 2 mm. long, tips acuminate, rather fragile and many broken off in older apothecia; disc smooth to somewhat unequal, densely white-pruinose when young, becoming cinnamon rufous to apricot orange.

Cortex 65–100 μ thick, fastigiate, hyphae 6–7 μ in diameter, lumen 3 μ, the outer 30 μ nubilated with minute brown crystals, gelified, the hyphae less clearly radial in the inner portion; algal layer about 40 μ thick, of predominantly radial filaments of *Trentepohlia*; medulla 30 μ thick, of coarse periclinal hyphae 6–7 μ in diameter, relatively thin-walled; axis 1550 μ in diameter, hollow, the wall 270 μ thick, of longitudinal hyphae 6 μ in diameter, lumen 2–3 μ, cavity 1100 μ in diameter, stuffed with branched brown, thick-walled hyphae, 6–7 μ in diameter, growing out of the wall.

In habit, this species suggests the DENSIROSTRAE, the hollow axis and red lower medulla suggest the subgenus EUMITRIA, although the presence of *Trentepohlia* algae clearly place it in the ROCCELLINAE.

UGANDA: Kigezi, Kasatoro forest, 1935–2560 m., on trees, *I. R. Dale L39*, at Kew.

7. USNEA LIECHTENSTEINII Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:211. 1897.

Type: Kenya, Machakos, *Liechtenstein & Poppischill*, saxicole.

Thallus 5–10 cm. tall, erect, caespitose, fruticose, rigid, citrine drab to deep olive buff, becoming brownish olive to Isabella color; holdfast blackened, sending root-like fibers about 0.5 mm. in diameter between the rock crystals, furnishing a common base for many primary axes; lower joint 5–10 mm. long, 1.5 mm. in diameter at the base, expanding upward to 2 mm. in diameter at the first dichotomy, several times dichotomous with very short internodes, then less frequently and irregularly so above; terete, cortex areolate, the areoles slightly foveolate below, then closely verrucose and subpapillate above, the verrucae sometimes in close rows but never distinctly angled, tips white but not perforate nor sorediate; ramuli irregularly disposed, thick, curving upward and subappressed, mostly 4–5 mm. long, nearly smooth, rather fragile and the obtuse tips often broken off.

Apothecia lateral, about 1 cm. back of the tips of the smaller branches, cupulate, 5–7 (–10) mm. in diameter; exciple smooth at first, becoming reticulate-rugose in relatively large areoles at maturity; marginal cilia erect, not dense, about 3 mm. long, then more spreading and annularly cracked, especially at the base, and often broken off at maturity; disc epruinose, buffy brown.

Cortex gelified, about 275 μ thick, the outer 25 μ obscured by brownish crystals, the hyphae thick-walled, branched and anastomosing but predominantly radial, 2.5–3 μ in diameter; algal layer about 50 μ thick, of *Trentepohlia* filaments, mostly radial, about 6 μ in diameter, cells cylindric, somewhat longer than broad, penetrating the cortex in bands and forming fracture planes between the areoles of the cortex; medulla 50–80 μ thick, of slender, very densely woven hyphae, heavily nubilated with minute brownish crystals, axis 750 μ in diameter, hollow, wall 250–300 μ thick, of very thick-walled, densely woven hyphae in a gel; cavity about 125–150 μ in diameter, irregular in outline, more or less stuffed with medullary hyphae which grow through the axis wall in radial strands about 150 μ wide, analogous to the rays of woody stems of flowering plants and perhaps performing the same functions.

TANGANYIKA: Dodoma Prov., Mt. Mpwapwa, 1610–1935 m., saxicole, *P. J. Greenway 2432*, at Kew; *2432a* in E. African Herb. (separated from the collection of *U. Dodomae* Dodge).

8. Usnea subcristata Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Tanganyika, Kondoa District, Swaga-swaga Hill, summit, 1775 m., on shrubs, chiefly *Tricalysia cacondensis, B. D. Burtt 891*, at Kew.

Thallus erect, very rigid, fruticose, 7–8 cm. tall, light brownish olive below, shading through Isabella color and honey yellow to chamois on the slender branches and ramuli, the upper ends of branches between chamois and deep olive buff; base and first branchings not seen as the plant has been glued to the herbarium sheet, and are obscured by several layers of branches; branch 7 cm. long, 2 mm. in diameter at its base, expanding to 3 mm. at the first lateral branch and then tapering slowly to about 1 mm. in diameter below the apothecium, rather densely ramulose, nearly terete in the lower two internodes; cortex subareolate, then coarsely papillate above, the papillae in predominantly longitudinal rows, making the branch angled, some of the papillae growing out to form ramuli; larger lateral branches similar to the main axis but 1–1.5 mm. in diameter; ramuli 1–15 mm. long, thick, tips rounded, the larger foveolate, the smaller nearly smooth; some of the larger ramuli may develop into slender lateral branches 0.4–0.5 mm. in diameter, sparsely papillate below, foveolate above, tips rounded.

Apothecia apparently terminal, nearly plane, up to 20 mm. in diameter; exciple smooth or papillate with radial ridges (as many as there are ridges at the top of the branch), smooth between; marginal cilia 2-ranked, subdistant, the outer rank coarse, often dichotomous above the base, tips acute, otherwise resembling larger ramuli, the inner rank slender, 1–2 mm. long, tips acute; disc vinaceous buff, or pale olive buff, pruinose.

Cortex variable in thickness, 50–90 μ, fastigiate, highly gelified, the outer 10 μ deeply staining; algal layer dentate outward, up to 40 μ thick, cells 6–7 μ in diameter, closely packed, protococcoid; medulla K—, about 130 μ thick, brownish, of densely woven hyphae with a narrow zone of loosely woven hyphae in the middle; axis 1400 μ thick, hollow, wall 300 μ thick, of longitudinal conglutinate thick-walled hyphae; cavity about 800 μ in diameter, more or less lined with a layer of thin-walled hyphae 10 μ in diameter, with deep brown contents; very loosely stuffed with hyaline thin-walled hyphae 5 μ in diameter, nubilated with hyaline crystals and a few hyphae similar to those lining the cavity.

This fertile highland species differs from the lowland, sorediose *U. cristata* in being a coarser plant with more but less sharply defined angles on the main axis and larger branches and in the more abundant, larger and subfoveolate ramuli.

9. Usnea elata Motyka, Lich. Gen. Usnea Stud. Monog. 57. 1936.

Type: Congo; M'pala, west shore of Lake Tanganyika, *Guillemé*.

Thallus 20 cm. long, probably erect, rather rigid, buffy olive to ecru olive; holdfast a coarsely verrucose disc 5–6 mm. in diameter, dark brown, giving rise to one or more main axes 2 mm. in diameter, with many small, short branches in the

lowest cm., then repeatedly dichotomous in the lower half, internodes about 1 cm. long, thinning at each dichotomy, axils complanate, nearly 90° angles, the branches soon erect before the next dichotomy, the internodes subterete to few-angled from low longitudinal or suboblique ridges, cracked and minutely isidiose, appearing farinose after the isidia are shed; in the upper two-thirds the ridges more irregular and anastomosing, giving a foveate appearance with minute isidiose verrucae between, the internodes more variable in length, some very short, giving a trichotomous appearance, others very long; summits long-capillaceous, rather fragile and broken off in our plants; eramulose (occasionally isidia grow out *in situ* forming groups of pseudoramuli 1–2 mm. long) or the small branches on the basal internode produce larger pseudoramuli from unequal dichotomies.

Apothecia rather rare, about 5 mm. in diameter, cupulate, sessile on the larger axes; exciple smooth to slightly impressed; marginal cilia moderately close, erect, variable in length up to 4 mm. long, the longer dichotomous near the tips, sparsely and minutely verrucose, perhaps finally isidiose; disc flesh color with a white pruina.

Cortex variable in thickness, 50–85 (–150) μ thick, gelified, loosely fastigiate, the outer 15 μ very dark brown; algal layer 30–50 μ thick, of discrete colonies of *Trebouxia*, cells 4–7 μ in diameter, forming a nearly continuous layer; medulla pink to rose color, I—, about 240 μ thick, quite closely woven next the algal layer, looser below (appearing dense under low magnification), hyphae 3–4 μ in diameter, lumen 1 μ; axis 840 μ in diameter, deep rose by reflected light, hyaline by transmitted light, slightly irregular in transverse section, wall about 200 μ thick, but cavity very irregular in outline (radiating sinuses), from the coalescence of many small cavities, about 30 μ in diameter, lined with larger thin-walled brownish hyphae, nearly hollow but traversed by an occasional hyaline hypha 6 μ in diameter, lumen 3 μ; wall hyphae longitudinal, very thick-walled, conglutinate, I slightly blue, especially next the cavity.

KENYA: Lake Ngunga, 1775 m., on trees, *G. M. Allen 1782*, in Howe herb. at Farlow Herb.

10. Usnea nana Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Kasatoro, Kabale River, 2256 m., corticole, *I. R. Dale L43 p. p. min.*

Thallus fruticose, erect, up to 4 cm. tall, deep olive to citrine drab; holdfast 2 mm. in diameter, conical, black, base 3–5 mm. tall, up to 1 mm. in diameter, black; once or twice dichotomous at the base, rarely dichotomous above; axes terete, up to 1 mm. in diameter below, tapering upward, smooth, densely ramulose, ramuli 1–2 mm. long, axils acute, tapering to a slender, obtuse, not blackened tip, not fragile, a few up to 4 mm. long, curved, rarely once-dichotomous; summits tapering to an acute tip, nude of ramuli in the upper 4 mm.

Apothecia sessile on the lower portions, of small secondary branches, cupulate, 1 (–2) mm. in diameter; exciple smooth; marginal cilia close, radiating, 1 mm. long,

resembling small ramuli but more fragile; disc concave, flesh color, white-pruinose.

Cortex 35–40 μ thick, of coarse conglutinate thick-walled predominantly radial hyphae 8 μ in diameter, lumen 3 μ (in places appearing pseudoparenchymatous); algae *Trebouxia*, in colonies 20–30 μ in diameter, in a nearly continuous layer, cells 7–8 μ in diameter; medulla up to 15 μ thick, of compact, periclinal thick-walled hyphae 3 μ in diameter; axis 800 μ in diameter, hollow, wall 150 μ thick, of slender thick-walled conglutinate hyphae; cavity 500 μ in diameter, very loosely stuffed with very thick-walled hyphae 3 μ in diameter.

11. Usnea firmula (Stirton) Motyka, Lich. Gen. Usnea Stud. Monog. 64. 1936.

Eumitria firmula Stirton, Scottish Nat. 6:100. 1881.

Type: Fernando Po, lava beds, G. *Thomson*, in the Art Galleries of the Glasgow Corporation.

Thallus about 10 cm. tall, rigid, ashy green, sparingly branched, closely ramulose; branches straight to somewhat flexuous, terete, 1–2 mm. in diameter, tapering somewhat above and below, thus appearing somewhat inflated, verrucose-papillate between the ramuli (perhaps only very young ramuli or scars of broken ramuli regenerating); main axes and bases of slender lateral branches densely ramulose, ramuli 5–15 mm. long, perpendicular, straight or slightly flexuous and arcuate, mostly annularly cracked at the base showing the rose medulla, tips slender but obtuse, not very fragile, breaking off near the tips; summits of slender lateral branches nude with abundant low white tubercles in our plants.

Apothecia terminal on lateral branches, 7–10 (–15) mm. in diameter, nearly plane; exciple convex, papillose, sometimes ciliate; marginal cilia rare, 5 mm. long, smooth; disc nearly plane, pale flesh color with a white pruina; epithecium dark; ascospores 8 × 10 μ, in narrow asci.

Migeod 419 is very old; the apical portions of most of the main axes are broken off, carrying away the apothecia. The color is between buffy brown and citrine drab rather than ashy green. The axis is black under the rose-colored medullar surface. It agrees in vegetative characters better with this species than with the sterile sorediose *U. implicita* (Stirton) Zahlbr. from the same region. The low white tubercles on the apical portions of the slender lateral branches may be initials of soralia but are not found on the main axes as are the soralia of *U. implicita*. *Dale L43* seems to be the juvenile stage of this species: It is only 3 cm. tall, the axis still solid, the medulla only partly rose color. It is sorediose and beginning to form an apothecium less than a mm. in diameter.

CAMEROONS: gully above Bamenda, 1930 m., *F. W. H. Migeod 419;* Cameroon Mt., 1610 m., *Dunlap;* above Buea, 1450 m., *F. W. H. Migeod 144;* all at Kew; *Bornmueller* misit Zahlbruckner sub *U. Baileyi*, in Howe herb., at Farlow Herb.

FERNANDO PO: lava beds, *G. Thomson*, type, in the Art Galleries of the Glasgow Corporation.

S. SUDAN: Onyiro, Issore, 1775 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57,* at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., on tree, very young, *I. R. Dale L43;* Bwamba Pass, 2250 m., on trees, *E. M. Shillito 90a;* both at Kew.

12. Usnea medio-africana Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

Thallus erect, subrigid, about 5 cm. tall; common holdfast about 7 mm. in diameter, flat, black, giving rise to 4–5 primary axes about 1.5 mm. in diameter; base very short, once or twice dichotomous with very short internodes and again dichotomous less than 1 cm. from the apothecia, mummy brown with dark olive buff ramuli; terete to slightly rugose, angular and subfoveolate; ramuli dense, 5–7 mm. long, very fragile and mostly broken off, the scars giving a coarsely verrucose to papillate appearance, smooth, annularly cracked, tips acute and minutely blackened.

Apothecia subterminal, up to 20 mm. in diameter, plane; exciple foveate, minutely verrucose, with radial ridges from concrescent ramuli; marginal cilia rather close, of variable length, up to 8 mm. long, the larger once dichotomous or sparsely ramulose; disc cinnamon, very slightly white-pruinose.

Cortex 60 (–100) μ thick, of predominantly radial, loosely woven slender hyphae in a gel, the outer 15 μ more densely woven and deeply staining; algal layer continuous, about 30 μ thick, of closely packed protococcoid cells; medulla 40 (–180) μ thick, white, pale rose next the axis, of very loosely woven, slender, thick-walled hyphae, more densely woven next the algal layer and the axis; axis 900 μ in diameter, solid at first becoming hollow, wall 180 μ thick, of slender conglutinate hyphae, cavity 550 μ in diameter, stuffed at first then hollow.

In sectioning the mature primary axes, the cortex and algal layer tear away from a thin layer of medulla next the axis, making it impossible to estimate the thickness of the mature medulla accurately. In *Hendrickx 4330* the medulla is 30–35 μ thick, compactly woven throughout.

This species is closest to *U. trullifera* Nyl. of Motyka's monograph and perhaps the atypical specimen cited by him from Tanganyika?. Mt. Mfimbwa, near Lake "Tanganyika-Nyassa", 2300 m., *From*, belongs here. Our plants differ from the Tahitian plants in being smaller with much larger apothecia and relatively thicker medulla.

uganda: Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.
congo: km. 30, route Kahusi, ramulicole, *F. L. Hendrickx 4330*, in E. African Herb.

13. Usnea brunnescens Dodge, Ann. Mo. Bot. Gard. 43:393. 1956.

Type: Uganda, Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

Thallus at least 10 cm. tall, fruticose, rather rigid, drying Mars brown to russet on the axes, younger ramuli cinnamon buff; holdfast a black disc about 7 mm. in diameter, giving rise to at least three branches, twice or thrice dichotomous with short internodes (1 cm. or less), then rarely dichotomous above, about 2 mm. in diameter in the lower half, then tapering to about 0.3 mm. at the densely ramulose blunt tip; cortex impressed and subareolate, nearly smooth in the lower internodes,

then very densely verrucose-papillate and ramulose above; ramuli 1–3 mm. long, single or in short oblique rows, but the branches not clearly angled, annularly cracked at the base and often the tips broken off, but seldom breaking away at the base to leave scars, the larger ramuli sparsely verrucose, producing single isidia on the verrucae, but not sorediate.

The tips of the branches end in a dense cluster of ramuli, perhaps a regeneration phenomenon following the breaking off of the end of the branch.

Cortex about 50 μ thick, of loosely woven, predominantly radial, slender hyphae in a gel, the outer half nubilated with minute hyaline crystals; algal layer about 40 μ thick, a nearly continuous layer of *Trebouxia* colonies, cells about 6 μ in diameter; medulla about 30 (–40) μ thick, of slender, very densely woven hyphae; axis about 1400 μ in diameter, hollow, wall 135 μ thick, of longitudinal, thick-walled conglutinate hyphae, lumen about 2 μ in diameter, cavity loosely stuffed with branched, anastomosing thick-walled hyphae up to 4 μ in diameter.

UGANDA: Kigezi, Mafuga, 2400 m., on trees, *I. R. Dale L41*, at Kew.

14. USNEA VERSICOLOR Motyka, Lich. Gen. Usnea Stud. Monog. 74. 1936.

Type: Cameroons, Cameroon Mt., 4040–4070 m., on volcanic ash, *Weberbauer*.

Thallus prostrate or subpendent, 20–30 cm. long, larger joints clay color to cinnamon buff, others light brownish olive, slender branches deep olive buff, base not seen, subarticulate, branching subdichotomous, the larger branch continuous at the axil, the smaller articulate and constricted, cracks narrow, dividing into joints not constricted at the ends but slightly inflated in the middle, somewhat flexuous, surface very slightly and indefinitely foveolate, with small round pseudocyphellae, or short, oblong, scarcely elevated farinose longitudinal ridges; main axes up to 1.5 mm. in diameter below, tapering above to the capillaceous summits; eramulose but the more closely dichotomous, very slender branches of the summits may simulate ramuli.

Our material from the same mountain at approximately the same elevation agrees well with Motyka's description except for the presence of inconspicuous pseudocyphellae and farinose ridges. As our plants are somewhat longer, perhaps they are older and these structures more developed. This species seems intermediate between the FOVEATAE and the ARTICULATAE.

CAMEROONS: Cameroon Mt., 4030 m., on bare rocky ground, *F. W. H. Migeod 196*, at Kew.

15. USNEA COMPLANATA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 109. 1936.

Usnea barbata v. *strigosa* f. *complanata* Müll. Arg., Hedwigia 31:276. 1892.
Usnea florida v. *strigosa* f. *complanata* Zahlbr., Cat. Lich. Univ. 6:574. 1930.
Usnea florida v. *strigosa* f. *pygmaea* Hue, Nouv. Arch. Mus. Paris IV. 1:35. 1899.
Usnea Schimperi Lenormand, herb. nom.

Type: Ethiopia, Debr; Eski, 2900 m., on trunks of *Euphorbia Collqual. W. Schimper*, 1852. The type of *U. florida* v. *strigosa* f. *pygmaea* Hue is: Ethiopia, Nahia in Machiha, 1930–2250 m., on *Euphorbia Collqual, W. Schimper 1022*, Nov. 1852.

Thallus erect, up to 3 cm. tall (only 1 cm. tall in our plants), snuff brown to Sayal brown; holdfast hemispheric, verrucose, 5 mm. in diameter, giving rise to several axes varying from nearly terete and foveolate, 2 mm. in diameter, to quite flat, 5 mm. wide, and deeply scrobiculate (resembling a small *Ramalina*), with 1–3 short flat secondary branches, rather densely ramulose in places, nearly nude in others, ramuli infundibuliform at the base, inflated and abruptly narrowed to an acuminate tip, 1–2 mm. long.

Apothecia up to 15 mm. in diameter, terminal, somewhat excentric; exciple foveate with sparse ramuli, some terete, some flattened; marginal cilia rather close, about 2 mm. long, resembling ramuli; disc somewhat concave, flesh color with a white pruina.

ETHIOPIA: M. Bachit, 2400 m., *W. Schimper 14*, ex herb Sbarbaro sub *U. Schimperi* Lenormand, at Farlow Herb. (duplicate cited by Motyka).

16. USNEA CORRUGATA Motyka, Lich. Gen. Usnea Stud. Monog. 105. 1936.

Type: Ethiopia, Podopolani, on *Euphorbia, Schweinfurth*, 1894.

Thallus subpendulous, up to 12 cm. tall, subrigid, brownish olive with ramuli and more slender branches partly buffy olive, very rarely dark red-maculate; base about 5 mm. tall, 2 mm. in diameter, expanding below into an irregular disc; holdfast 4 mm. in diameter, densely sympodially branched just above the base, axils only slightly flattened; branches perpendicular or nearly so, curving apically, secondary branches 10–15 mm. long, nearly 2 mm. in diameter, then trichotomous with greatly flattened axils, then more closely dichotomous or irregularly branched, the branches about 1 mm. in diameter, upper ones 0.5 mm. or less, deeply foveate throughout, the larger rugi longitudinal, acute, bearing dense pale greenish isidiose soredia; ramuli very irregular, often in dense groups on the smaller branches (perhaps from isidia germinating *in situ*), the longer ramuli branched, subarticulate and inflated; summits quite closely divergently branched, tips obtuse. Apothecia not seen.

UGANDA: Kigezi, Kabale, 1960 m., corticole, *I. R. Dale L1*, at Kew.

17. USNEA PULVERULENTA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 107. 1936.

Usnea barbata v. *pulverulenta* Müll. Arg., Flora 68:499. 1885.
Usnea florida v. *pulverulenta* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1888/89: 1945. 1890.

Type: Ethiopia, Bagla, 2410 m., *Hildebrandt*, 1885.

Thallus fruticose to subpendent, over 6 cm. long (only 4 cm. in our plants), rather flaccid, axis wood brown, ramuli deep olive buff; holdfast a verrucose brownish disc 2 mm. in diameter, base 1 mm. tall, 1 mm. in diameter; dichotomous with internodes 5 mm. long below, 1 mm. in diameter, terete, smooth between the rather dense ramuli, tuberculate to subpapillate above, thinning at each dichotomy, with granular farinose soralia, subfoveolate between, ultimate branches slender, acuminate but rather short; ramuli dense throughout, mostly about 2 mm. long, some 3–5 mm., probably small secondary branches, tuberculate and sparsely ramulose, slightly inflated, tips acute.

Cortex 80 μ thick, gelified, fastigiate, almost pseudoparenchymatous, cells about 4 μ in diameter, 6–7 μ long, rather thin-walled below, thicker-walled above with very narrow lumina; algal layer 20–35 μ thick, of *Trebouxia*, cells 7–10 μ in diameter, somewhat angular from mutual pressure; medulla about 225 μ thick, the outer half of densely woven predominantly periclinal hyphae, the inner half of predominantly radial, very loosely woven hyphae about 4 μ in diameter, sparsely nubilated with hyaline granules, K— or faintly yellow (the axis tears loose from this inner zone in sectioning, making measurement of the thickness of the medulla inexact); axis 350 μ in diameter, of conglutinate predominantly longitudinal thick-walled hyphae.

Although placed by Motyka in the FOVEATAE, it might equally well be placed in the GLABRATAE, PYCNOCLADAE, near *U. ruwenzoriana* Motyka, as the branches are not, or only very slightly, foveolate above, and the color becomes fuscous in the herbarium; the branches are more densely ramulose than is usual in the FOVEATAE.

ETHIOPIA: Bagla, 2410 m., *Hildebrandt*, 1872, ex herb. Sbarbaro at Farlow Herb.

18. USNEA FLAVESCENS Motyka, Lich. Gen. Usnea Stud. Monog. 125. 1936.

Type: Kenya, Ngongo Bagas, 2700 m., *A. G. Allan.*

Thallus pendent, flaccid, up to 60 cm. long, pale olive buff (in our material), finally becoming pale stramineo-fuscous (*fide* Motyka); holdfast short-conic, black, base slender, about 10 mm. long, 0.8–1 mm. in diameter, 3- to 4-annulate, then more or less frequently dichotomous, often unequally so throughout, articulate, the joints 6–30 mm. long, constricted at the ends, cracks narrow, partly slightly foveate, abundantly so on some joints, very rarely so on others, cortical cracks (pseudocyphellae) rare, inconspicuous, increasing rapidly to 2–2.5 mm. in diameter and decreasing slowly to the almost non-articulate, capillaceous summits; the larger branches somewhat flexuous, sparingly ramulose, sometimes several consecutive joints eramulose; the smaller branches more closely ramulose (imitating a small *U. longissima*); the ramuli of the larger branches up to 1 cm. long, sometimes branched and spinulose; the ramuli of the smaller branches 1–2 mm. long, usually articulate at the base, tips acute and sometimes blackened.

Apothecia sessile on small secondary branches, 2–2.5 mm. in diameter, plane; exciple shallowly foveate; marginal cilia in two ranks, the inner rather close, 1–2

mm. long, suberect, the outer rank subdistant, 3–4 mm. long; disc flesh color, slightly white-pruinose (based on *Curtis 669* from Kenya).

Greenway 3816 is a mixture of several species. On one of the two sheets at the E. African Herbarium is a single plant which seems to be this species, but the color is now (after 21 years) between snuff brown and Sayal brown throughout; some of the joints are very foveate; ramuli more abundant on the larger joints and less so on the capillaceous summits, most of which have been broken off in collecting.

ERITREA: Habab, Tsertsera, *F. Gallina*, ex herb. Cufino at Farlow Herb.

ETHIOPIA: Simien, Mindigabsa, ramulicole, *H. Scott 323*, at Kew.

KENYA: Mt. Kenya, 2250–2575 m., on bamboo twigs, *G. M. Allen 1797*, in Howe and Riddle herbs.; trail from West Kenya Forest Station to summit of Mt. Kenya, 3630 m., *Edgar A. Mearns 1522* (T. Roosevelt Exp.); 40 miles southeast of Narok, 2250 m., *Anita Grosvenor Curtis 669*; all at Farlow Herb.

TANGANYIKA: Kilimanjaro, Bismarck Hill, 3220 m., *P. J. Greenway 3816 p. p. min.*, in E. African Herb.

19. USNEA PRAELONGA Stirton, Scottish Nat. 6:107. 1881.

Type: South Africa, without locality, *J. H. McLea*, in Brit. Mus.

Thallus pendent, flaccid, up to 60 cm. long, gray to yellowish gray, drying dark olive buff to deep olive buff or colonial buff in recent collections to chamois in older collections (Isabella color in the type), lighter on the capillaceous summits; densely dichotomous at the holdfast, branches about 0.5 mm. in diameter, scarcely inflated in the lowest cm., then articulate, joints 5 (–10) mm. long, 2 (–3) mm. in diameter, then sparingly and irregularly dichotomous for the next 30 cm., then repeatedly dichotomous, the joints abruptly more slender and almost cylindric, rather densely dichotomous at the summits; eramulose or very rarely ramulose in the capillaceous summits; surface smooth to somewhat impressed or foveate on the larger joints, pseudocyphellae very inconspicuous, scarcely visible under 10 × magnification, the slender branches minutely foveate with the cortex cracking along the ridges. No apothecia nor soredia seen.

Associated on the sheet of *Gillett 4708* are evidently juvenile plants, the joints not inflated, the surface more foveolate, resembling the smaller branches of the larger plants. *Glover & Gilliland 476* are shorter plants, tawny olive to clay color (collected in 1944), but they seem to be this species rather than *U. articulata* v. *Kotschyana* Motyka from Syria, which they resemble in color.

In the Eritrea to Somaliland region, this species seems confined to *Juniperus*, and the Somalis consider it a part of the juniper tree, it is so constantly associated. The natives use it as a stuffing for pillows and beds. The Ishaak tribes call it *sarokh* or *jeban*.

ERITREA: Filfa forest, *P. E. Ellis 5*, at Kew.

SOMALIE FRANÇAISE: Dai, 1450 m., *G. Popov 1296* (Desert Locust Survey).

BRITISH SOMALILAND: without locality, *R. S Taylor*, Aug. 1927; Libah Mts., Wawanak Peak, 1900 m., 10° 20′ N., 43° E., *J. B. Gillett 4708* (Abyssinia-Somaliland Bound. Comm.); Surud Range, Shimba Beris, 10° 45′ N., 47° 12′ E., *Collenette 402*; Wagar Range, Taisaiver mist belt, *P. E. Glover & H. B. Gilliland 476*; all at Kew.

SOUTH AFRICA: without locality, *J. H. McLea*, type, in Brit. Mus.

20. Usnea pseudocyphellata Motyka, Lich. Gen. Usnea Stud. Monog. 125. 1936.

Type: Cameroons, Buea (Bula in Motyka, *lapsus*?), on old trees, *Deistel.*

Thallus pendent, flaccid, up to 40 cm. long, tawny olive to pinkish buff, summits deep olive buff; base about 5 mm. long, 0.6 mm. in diameter, narrowly blackened below, repeatedly dichotomous in the lower 2 cm., then less so until the capillaceous 7–8 cm., where the internodes are again short; articulate, flexuous, joints 0.3–20 mm. long, mostly about 10 mm. and up to 2 mm. in diameter throughout, tapering only slightly apically and narrowing abruptly to 0.5 mm. or less at the capillaceous summits, constricted at the ends; surface impressed or subfoveolate, pseudocyphellae rare, punctate or in short, very low ridges on the main axes, more abundant and elevated on the smaller secondary branches, farinose, white to pale yellow; ramuli rare, slender, up to 10 mm. long on the main axes, apparently from unequal dichotomies on the capillaceous summits.

Apothecia lateral, 5 (–10) mm. in diameter, cupulate, becoming plane; exciple smooth or with a few periclinal cracks near the margin; marginal cilia few, up to 20 mm. long, slender, subtuberculate with pseudocyphellae; disc chalky white, pruinose, becoming carneous as the pruina weathers away.

sierra leone: without locality or collector at Kew. Evidently a very old specimen, Verona brown with tawny olive summits, sterile with somewhat shorter joints. In habit it resembles *U. atlantica* Motyka from the Canary Islands, which is said to remain pale stramineous in the herbarium. Motyka cites a specimen from the Canary Islands collected by Humboldt sub *Lichen hirtus* v. *Pini* which must have been over a century old.

cameroons: Mt. Cameroon, 1610 m., *Dunlap*; above Buea, 1290 m. and 1450 m., *F. W. H. Migeod 53, 144* respectively, at Kew.

21. Usnea speciosa Motyka, Lich. Gen. Usnea Stud. Monog. 124. 1936.

Type: Ilha São Thomé, 1300–2100 m., *A. F. Möller.*

Thallus pendent, rather rigid, up to 30 cm. long, drying pale ashy fuscous (Motyka, in our material VanDyke brown to Sayal brown [Fernando Po], tawny olive [Cameroons]); base 3 mm. long, 0.5 mm. in diameter below, expanding upward; dichotomously or sympodially branched once or twice with short internodes, then rarely dichotomous; articulate, joints up to 7 cm. long, 2–2.5 m. in diameter (only 1 mm. in diameter in specimen from 2900 m.), curved to falcate, sharply constricted at the ends, but cortex often continuous; terete, cortex with short, longitudinal or somewhat oblique cracks, farinose, mostly pale sulfur yellow, foveolate, with small punctate pseudocyphellae, not elevated; ramuli occasional on the secondary branches, very rare on the main axes (perhaps only an undeveloped secondary branch); summits abruptly capillaceous, branches 0.4–0.5 mm. in diameter, tapering distally, rather densely dichotomously branched.

Melliss 21, from St. Helena, is apparently the basal portion of an old specimen, about 10 cm. long, hazel to russet with elevated farinose soredia. After years in

the herbarium it has stained the paper to which it is glued, testaceous.

SIERRA LEONE: Loma Mts., Galerie Forest, 1800 m., on *Tridactyla, P. Jaeger 4283,* at Kew.

CAMEROONS: Buea, Musaka swamp, 1610 m., *T. D. M. 696;* Victoria, Meyer Crater, 2575 m., *T. D. M. 917;* both at Kew, ex Hb. Bot. Gard. Victoria, Cameroons.

FERNANDO PO: 640 m., 1610 m. and 2900 m., *Gustavo Mann;* all at Kew.

ST. HELENA: without locality, *J. C. Melliss 21,* at Kew.

22. USNEA VESICULATA Motyka, Lich. Gen. Usnea Stud. Monog. 114. 1936.

Type: Tanganyika, R. Uusoro [Wusiro?], in swamp, 2600–3000 m., *Stuhlmann.*

Thallus pendent, up to 60 cm. long, flaccid, main axes drying buckthorn brown to yellow ochre, capillaceous summits between chamois and deep olive buff; holdfast of rooting fibers, repeatedly dichotomous at the top, then sparingly dichotomous on the main axes, thinning at each dichotomy and again closely dichotomous at the base of the capillaceous summits; articulate, joints inflated, 2 mm. in diameter, 10–20 mm. long below, shorter on the main axes above, the capillaceous summits nearly cylindric, but the cortex annularly cracked; surface smooth to impressed or foveate on the larger joints, pseudocyphellae punctate or oblong, farinose, very inconspicuous; eramulose on the main axes, sparingly and irregularly ramulose on the summits, ramuli slender, up to 2 mm. long, often black-tipped.

Apothecia infrequent, not seen in our material, lateral on slender branches, rarely subterminal, 2–4 mm. in diameter, thin, plane; exciple lacunose, marginal cilia few but comparatively long, capillaceous; disc plane, flesh color, slightly pruinose, thecium 60 μ tall; asci narrow; ascospores uniseriate, $10 \times 11\ \mu$, with a distinct epispore.

The material referred here is not uniform. Sometimes a collection, or plants separated from the same collector's number, are much darker, russet to Dresden brown, and the joints of the main axes only about 1 mm. in diameter, surface less impressed and foveate, pseudocyphellae in very low verrucae (visible with 12× magnification). More field work will be necessary to decide whether they may belong to a different species. In the following list of specimens, they are marked with an asterisk (*) preceding

KENYA: Longondoti, crater forest, 2575 m., arboricole, *R. A. Dummer 5308,* at Kew.

UGANDA: Bugishu, Butandiga, 2415 m., *A. S. Thomas 484;* Elgon Madangi, 3550 m., *A. S. Thomas 607*; Kigezi, * Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Mgahinga, 3380 m., *A. S. Thomas 2457* (both forms); Mafuga, 2575 m., *I. R. Dale L42*; all at Kew.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4300, 4305, 4316*; km. 30, route Kahusi, *F. L. Hendrickx 4330,* a fragment; all in E. African Herb.

ANGOLA: Cuanza Sul, Amboina, Capir near the Carloaongo River, *J. Gossweiler 9991 p. p. min.,* juvenile, at Kew.

TANGANYIKA: Kilimanjaro, near Bismarck Hill, 3220 m., in evergreen mist forest, *P. J. Greenway 3816* (both forms); * Dabaga, *Dr. Geilinger 1947, 6.IX.32*; at Kew.

NYASALAND: Nyika Plateau, ramicole, 2340 m., *L. J. Brass 17215,* in N. Y. Bot Gard. Herb.

23. USNEA DEMINUTA Motyka, Webbia 8:389. 1952.

Type: Ethiopia, Alto Semièn, Beleghes, Reg. Sancaber, 3300 m., *Pichi-Sermolli 2907*.

Thallus flaccid, pendent, 10–15 cm. long in type (more than 30 cm. long in our material), drying buckthorn brown on main axes, to yellow ochre or clay color on smaller branches; base absent in our plants, main axes 0.5–0.6 (–1) mm. in diameter, tapering upward; terete, articulate, many of the larger joints impressed to foveolate or even perforate, epapillate, up to 10 mm. long, mostly shorter, constricted at the ends, cracks narrow but showing the medulla or axis, the slender branches usually continuous, only slightly articulate, irregularly dichotomous; ramuli rare on the larger joints, occasional on the more slender branches, perhaps only undeveloped branches from an unequal dichotomy, and rare spinules which break away leaving minute scars and probably serve as isidia; pseudocyphellae minute on the larger joints, also short longitudinal or oblique cracks in the cortex through which medullary hyphae protrude.

Tangled with *Mearns 1776* is a fertile terminal fragment which seems to be this species. The axis is orange cinnamon shading to light vinaceous cinnamon at the tips, and is regularly annularly cracked, exposing the white medulla; the joints cylindric, rarely very slightly inflated and faintly longitudinally rugose with rare pseudocyphellae; the smaller branches show more pseudocyphellae and longitudinal cracks. The apothecia are 2–4 mm. in diameter, cupulate, sessile; exciple smooth except for several very deep, rounded foveolae on either side of the concrescent branch; marginal cilia distant, of variable length, the shorter nearly erect, the longer spreading and curved, about 5 mm. long, annularly cracked at the base with a few very minute pseudocyphellae; disc very concave, white-pruinose.

Our specimens have been referred here although the dimensions are slightly larger and I have seen no material from Ethiopia. They have been found tangled with other much larger species of the section ARTICULATAE, but do not resemble the juvenile forms of those species.

KENYA: west slope of Mt. Kenya, trail from West Kenya Forest Station to summit, in bamboo zone, ca. 3000 m., *Edgar A. Mearns 1776* p. p. (T. Roosevelt Exp.), at Farlow Herb.

UGANDA: Imatong Mts., Mt. Kineti, 2810 m., ramulicole, *A. S. Thomas 1873*, at Kew.

TANGANYIKA: S. Pare Mts., Mtonto, 2100 m., on bushes of *Philippia, P. J. Greenway 6532a*, in E. African Herb.

24. USNEA ARTICULATA (L.) Hoffm. subsp. AETHIOPICA Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Ethiopia, below Debra Erki, on fir, *Schimper 18*, 21 Oct. 1850, det. *U. articulata* v. *intestiniformis* Ach. by Müller Argau.

Thallus pendent, more than 25 cm. long, probably flaccid (now glued tightly to herbarium sheet), snuff brown; base about 1 mm. in diameter, 8 mm. long, annulate, not blackened, then about twice closely dichotomous and occasionally so

throughout; articulate, joints irregular in size in the same axis, straight or curved and cucumiform, the larger joints mostly basal but not always so, 25–30 mm. long, 4–5 mm. in diameter (crushed flat in drying and hence appearing up to 7 mm.), the smaller joints 5–10 mm. long, about 1–1.4 mm. in diameter, usually straight, occasional branches long and slender, scarcely articulate and occasionally quite closely ramulose; ramuli slender, about 5 mm. long; the larger joints often foveate to scrobiculate, with small slightly elevated pseudocyphellae, sometimes in rows, the smaller joints smooth with minute pseudocyphellae; the smallest almost non-articulate branches with small soralia of isidiose soredia.

Superficially our pressed plant, glued tightly to the herbarium sheet, resembles subsp. *intestiniformis* (Ach.) Crombie, in habit and color. The latter grows on sandy soil in England, France, Belgium, and the Netherlands. The main axes are more uniform in diameter and larger with relatively shorter joints, pseudocyphellae quite rare, and no soralia have been observed. Our plant is apparently more closely related to subsp. *Kotschyana* Motyka from Syria, 40 cm. long, with joints smaller and more uniform in size, coarsely papillate and sorediose. I am unable to estimate the size of our plant as the upper portion of the main axes has been broken away; the portion present measures 25 cm. long.

ETHIOPIA: below Debra Erki, on fir, *Schimper 18*, 21 Oct. 1850, det. as *U. articulata* v. *intestiniformis* (Ach.) Crombie, at Kew.
KENYA: Gilgil, on trees, *G. M. Allen 1780*, in Howe herb. at Farlow Herb.

25. USNEA TERRESTRIS Motyka, Lich. Gen. Usnea Stud. Monog. 75. 1936.

Type: Tanganyika, Mt. Kilimanjaro, 4000 m., on rocks in grassland, above tree-line, *H. Meyer*.

Thallus prostrate or pendent, pale gray green when fresh, drying tawny olive on larger branches to warm buff on the capillaceous summits, up to 20 cm. long, base very dark brown, about 1–3 mm. in diameter and 1 mm. tall, fraying out below into many root-like fibers enclosing soil particles and expanding above to 2 mm. in diameter at the first fork; dichotomous, constricted at the axil, articulate, joints 7–20 mm. long, constricted at the ends, lower joints inflated to 2 mm. in the middle, the upper ones to 1 mm., separate or cortex continuous, tapering with closer ramuli and repeatedly dichotomous branching to the capillaceous summits, tips of ultimate branches acute, slightly blackened; surface smooth to impressed and subfoveate, becoming nearly terete at the summits; ramuli rare on the larger branches, perpendicular, straight or slightly curved, articulate at the base but not inflated, tips acute, longer, and more slender, abundant on the summits but never crowded, mostly 5 mm. or less long, a few much longer, subtuberculate and occasionally pseudocyphellate; pseudocyphellae white, very small and inconspicuous, round or elongate; soredia clearly seen only on James' specimen from Kenya, abundant on smaller branches, from rather large, farinose, pale sulfur soralia, hemispheric, rarely crateriform when eroded, very rarely substipitate.

The above description is based mostly on *Turrall 71* from the type locality, as the specimen agrees well with Motyka's description although a little larger and with inconspicuous pseudocyphellae, easily overlooked, and with soralia. *Burtt 4071* from Mt. Meru is a tangled mass of many plants with fragments of dead mosses glued to the herbarium sheet. The one plant I succeeded in disentangling appears smaller and younger, only 11 cm. long, but is morphologically similar. Burtt's specimen from Ruanda is a fragment, slightly darker, mostly terete, rarely impressed, with very rare pseudocyphellae. Apparently broken smaller branches and the ultimate branches are capable of forming a new holdfast and continuing to develop new secondary axes. Burtt's specimen seems to be a fragment of one of these secondary axes.

James' specimen from Kenya is a mass of plants glued to the herbarium sheet, evidently terrestrial, as the mass contained a small pleurocarpous moss, bits of dead leaves, and very rotten twigs, dead grasses and scraps of *Parmelia.* The plants are tawny olive to Sayal brown, the capillaceous summits cinnamon buff to chamois, the joints on some of the principal axes 20 mm. long, 6.5 mm. in diameter (up to 10 mm. when pressed flat), thus suggesting *U. articulata* subsp. *aethiopica* Dodge, but these large joints are shorter and foveate and occasionally with a small soralium, or a short farinose ridge; soralia abundant and well developed on the smaller branches.

KENYA: Aberdare Mts., *Sir Evan James,* 1905, at Kew; w. slope of Mt. Kenya, 4200 m., *Edgar A. Mearns 1654* (T. Roosevelt Exp), in Mo. Bot. Gard. Herb., det. Motyka, and at Farlow Herb.

TANGANYIKA: Kilimanjaro, Bismarck-Peters, 3420 m., *R. G. Turrall 71,* at Kew and E. African Herb.; ober Waldrand, 3000 m., *Dr. Geilinger,* at Kew; Arusha District, Mt. Meru, 4680 m., *B. D. Burtt 4071*; at Kew; all on volcanic rocks in alpine meadows above tree line.

CONGO: Ruanda, Mufumbiro Mts., Mt. Mikeno, among grasses, *B. D. Burtt,* at Kew.

26. USNEA RUGOSA Motyka, Lich. Gen. Usnea Stud. Monog. 113. 1936.

Type: Ethiopia, Bagla, 2700 m., *Hildebrandt.*

Thallus pendent, flaccid, up to 65 cm. long, olive buff on the main axes, pinkish cinnamon on slender branches in recent specimens (2 years old), finally light brownish olive to Isabella color on the main axes, lighter on slender branches in older specimens (22 years old); holdfast inconspicuous, base up to 15 mm. long, 0.6–1 mm. in diameter, infrequently dichotomous throughout; articulate, joints mostly 2 mm. in diameter on main axes with an occasional joint up to 4 mm., varying in length from 2 to 10 mm.; surface variable, some joints smooth, terete, others with inconspicuous pseudocyphellae and low, narrow, farinose, more or less longitudinal ridges, the larger joints somewhat compressed and foveate with dense patches of dichotomous ramuli which may grow out to form the long secondary, capillaceous branches, up to 15 cm. long, surface asperate with punctiform soralia, somewhat larger and isidiose soralia on some of the basal joints; pseudoramuli arising from unequal dichotomies in the slender portion of the thallus.

Only lateral apothecial initials seen in our material. Motyka describes the apothecia as lateral, about 5 mm. in diameter, exciple very thin, plane, smooth; marginal cilia small, variable in length, flexuous, articulate; disc nearly plane, rugose; thecium 60 μ tall; asci ventricose; ascospores 7×9 μ, with a thin epispore.

Hildebrand 307 at Kew seems to be this species; the color is uniformly clay color, mostly with a white pruina from excess of mercuric chloride in poisoning; the main axes are rather more slender and smoother, sterile. It may be a duplicate of the type or perhaps of the specimen cited by Motyka as *U. articulata* subsp. *mediterranea* Mot. which, however, remains pale stramineous or very pale olive fuscous in the herbarium. There is a discrepancy in the elevation cited for the type; in the citation before the description, Motyka gives 2700 m., while in the citation of specimens seen at the end he gives 2420 m. The specimen at Kew is given as 7500 ft. (2420 m.).

ETHIOPIA: Galla Pass, 9° 28′ N., 42° 19′ E., *J. B. Gillett 5130*, Abyssinia-Somaliland Bound. Comm.; Simien, Mindigabsa, *H. Scott 323*; Bagla, 2420 m., *J. M. Hildebrandt 307;* all at Kew.

27. USNEA VAINIOANA[1] Zahlbr., Cat. Lich. Univ. 6:597. 1930.

Usnea fragilis Vainio, Hedwigia 37:40. 1894, non Stirton. 1882.

Type: Uganda, Mt. Ruwenzori, 0° 5′ S., *Scott-Elliott.*

Thallus up to 30 cm. long, pendent, very flaccid, rather fragile when dry, between colonial buff and olive buff, one group of plants cream buff after drying; base 5 cm. long, 0.6 mm. in diameter, annularly cracked; holdfast conic, 1 mm. in diameter, black; main axes 0.6 mm. in diameter, tapering gradually at each dichotomy to long capillaceous summits; branching infrequently dichotomous, the larger branches articulate, joints up to 5 mm. long, not or very slightly inflated below, not constricted at the ends, terete or very slightly impressed to subfoveolate, smooth, eramulose (less-developed branches may simulate ramuli); summits capillaceous, flexuous. Apothecia and soredia not seen in certain material.

Turrall 55 in the E. African Herbarium and a fragmentary plant untangled from another species in specimens from Kew seem to be this species. The main axes are up to 1 mm. in diameter, the joints somewhat more inflated, some slightly more foveolate or very slightly rugose; medulla K—. Apothecia very rare, lateral on smaller branches, 0.3 mm. in diameter, exciple subimpressed, very slightly pruinose; disc plane, 2 mm. in diameter, pale carneous, densely white-pruinose with 6–8 marginal cilia of variable length. This plant seems to be intermediate between *U. Vainioana* Zahlbr. and *U. exasperata* (Müll. Arg.) Vainio.

ETHIOPIA: Simien, Mindigabsa, *H. Scott 323a;* Geech, *H. Scott 250;* both at Kew.

TANGANYIKA: Mt. Kilimanjaro, 2900–3030 m., on giant heather, *R. G. Turrall 55,* in E. Africa Herb., fragment at Kew; S. Pare Mts., Mtonto, 2100 m., *P. J. Greenway 6532,* in E. African Herb.

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., ramicole, *L. J. Brass 16846* (Vernay Nyasaland Exp.), in N. Y. Bot. Gard. Herb.

[1] Original spelling *Wainioana* corrected by Motyka (Lich. Gen. Usnea Stud. Monog. 437. 1937) to conform to Vainio's preference for spelling his name after the Finnish revolution.

28. Usnea gracilis Ach., Lichenogr. Univ. 627. 1810.

Type: Ile Réunion (Bourbon), com. *Weber & Mohr.*

Thallus pendent, up to 30 cm. long, flaccid, gray to pale green, becoming deep olive buff in the herbarium; the main branches often Natal brown or darker in the lower portion; base hemispheric, attached to the bark; immediately dichotomous and repeatedly so throughout, often unequally so when one branch resembles a long, slender curved ramulus; lower portion of the main axes about 0.7 mm. in diameter, gradually tapering to the capillaceous summits; terete, continuous or annulate with very minute cracks, smooth, with rather indistinct paler lines; soredia unknown.

Apothecia very rare, sessile on smaller branches, up to 4 mm. in diameter, cupulate to subplane; exciple smooth; marginal cilia distant, 2–10 mm. long, annularly cracked at the base, tapering to acute tips; disc flesh color, faintly white-pruinose.

Cortex 90 μ thick, fastigiate, highly gelified; algal layer about 40 μ thick, cells protococcoid, 6–7 μ in diameter, dying in the older portions of the thallus and leaving cavities; medulla 225 μ thick, of densely woven hyphae 3–4 μ in diameter, lumen 1 μ; axis 275 μ in diameter, of conglutinate, thick-walled longitudinal hyphae. As the duplicate of *A. G. Allan* from Kenya in Herb. Bouly de Lesdain is cited by Motyka, probably his statement "medulla tantum ca. 20 μ crassa" is a misprint for 200 μ.

ETHIOPIA: without locality, *J. Omer-Cooper*, at Kew.

KENYA: Ngongo Bagas, *A. G. Allan*, com. Rev. W. Lillie, in Howe herb. at Farlow Herb.

TANGANYIKA: E. Usambara, Amani-Maramba, 1030 m., *P. J. Greenway 4151.*

CONGO: Mt. Kahusi, ca. 2700 m., on *Arundinaria alpina*, *F. L. Hendrickx 4300, 4302, 4314*, sparingly fertile, in E. African Herb.

NYASALAND: Mt. Mlàngi, 1450–2250 m., *P. J. Greenway 6332.*

MAURITIUS: without locality or collector, ex herb. Macreight in Tuckerman Herb., sub *U. plicata* at Farlow Herb.

RÉUNION: com. Müller Argau, at Farlow Herb.

29. Usnea pulchella Motyka, Lich. Gen. Usnea Stud. Monog. 442. 1937.

Type: St. Helena, Diana Peak, *Dumont d'Urville*, at Uppsala, not seen.

Thallus pendent, very flaccid, 25 cm. long (45 cm. in our specimens), drying bister to snuff brown on the main axes, pinkish cinnamon to cinnamon buff on slender branches and ramuli; holdfast a small black disk under the outer layers of bark cells, the base growing outward through a crack, 10 mm. long, 1 mm. in diameter, curving downward, annularly cracked, the part within the bark black; repeatedly dichotomous throughout, internodes somewhat shorter near the base and in the capillaceous summits; larger branches articulate, joints of variable length and diameter, some slightly inflated, up to 1.3 mm. in diameter, mostly about 1 mm. in diameter, others on the same branch shorter, cylindric, about 0.8 mm. in diameter, smooth, or on the slenderer, less articulate branches, very minutely white tuberculate (or pseudocyphellate?); the larger branches almost

eramulose, the slender branches quite irregularly ramulose; ramuli 10–40 mm. long, the shorter slender, straight or curved and smooth, the longer somewhat tuberculate and occasionally once or twice dichotomous (perhaps arrested development of a branch), usually flexuous; sometimes several growing out at a "node" forming a tuft (as in *U. nidifica*) in the type, absent in our specimens.

It seems quite likely that *U. monumenti* Fée,[1] type from St. Helena, trees about Napoleon's tomb, without collector, is the same species, but I hesitate to reduce *U. pulchella* Motyka to synonymy without seeing the types. *U. Lyngei* Motyka, from the same locality as *U. monumenti* Fée, has minute white farinose tubercles and ramuli not in dense clusters. *U. umbrata* Motyka, also from St. Helena, is very rigid and less articulate.

Our plants are longer and somewhat more slender than the type (*fide* Motyka) and have minute white tubercles which probably develop a few isidiose soredia. Perhaps the tufts of ramuli mentioned by Motyka are such isidiose soredia which have developed *in situ*. Otherwise our plants agree well with Motyka's description.

FERNANDO PO: Santa Isabel Peak, 2900 m., *Gustavo Mann 682*, probably arboricole, 2 sheets at Kew.

30. USNEA MONILIFORMIS Motyka, Lich. Gen. Usnea Stud. Monog. 447. 1937.

Type: S. Africa, Natal, hills above Mauritzburg, *Anton Rehmann*.

Thallus pendent, up to 30 cm. long, flaccid, lower portions of main branches sepia shading upward to cream buff at the summits, somewhat shining; holdfast a disc 2 mm. in diameter, base blackened, about 2 mm. long, 0.5–0.7 mm. in diameter; several times dichotomous near the base, some of the secondary branches forming holdfasts, then less closely dichotomous throughout; eramulose (occasionally one branch develops more slowly and resembles a ramulus); main branches 0.5–0.7 (–1) mm. in diameter, thinning at each dichotomy, summits capillaceous; terete, closely annulate, joints 1–3 (–10) mm. long, not constricted at the ends, cracks narrow, white-margined; very smooth, variegated with white points and lines (pseudocyphellae ?), very rarely the lines are slightly elevated.

Superficially, this species somewhat resembles *U. gracilis* with somewhat the same geographic distribution at low elevations, but with a thicker, laxer medulla and darker fuscous color. If the white points and lines are considered as pseudocyphellae, it would suggest inclusion in the ARTICULATAE instead of the STRAMINEAE-AMOENAE and a relationship to *U. deminuta* Motyka from Ethiopia at much higher elevations.

KENYA: Ngong hills, 2370 m., *P. R. O. Bally B94;* Marsabit Mt., *A. T. A. Ritchie*, com. *P. R. O. Bally B1416*; at Kew.

TANGANYIKA: Kilimanjaro, near Bismarck Hill, 3220 m., in evergreen mist forest, *P. J. Greenway 3816;* Marangu, Bismarck, 2140 m., *R. G. Turrall 37*, at Kew.

CONGO: Mt. Kahusi, 2700 m., on Ericaceae, *F. L. Hendrickx 3440*, in E. African Herb.

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[1] In Dictionnaire Classique (ed. Bory de St. Vincent) 16:481. 1830.

31. Usnea straminea Müll. Arg. emend. Motyka, Lich. Gen. Usnea Stud. Monog. 466. 1937; Müll. Arg., Flora 62:162. 1879, p. p. excl. syn.

Type: Mauritius, *Robillard* at Genève, a portion in Farlow Herb., selected by Motyka as type. The New Zealand specimen from Nelson, com. Ferd. v. Müller, also cited by Müller Argau, is referred by Motyka to his var. *substraminea* as well as the types of the synonyms cited by Motyka.

Thallus pendent, more than 20 cm. long, somewhat flaccid, pale stramineous when fresh, main axes drying hazel or lighter, ramuli warm buff, shining; holdfast and base broken off in material available; several times closely but somewhat unequally dichotomous near the base, then rarely so above, axils about 90° angles, the branches curving downward, nearly parallel, about 1 mm. in diameter, somewhat flexuous, annularly cracked and subarticulate, terete, some joints not constricted at the ends, some with surface slightly foveate, and some sparsely low-tuberculate (probably initials of ramuli); secondary branches 0.3–0.5 mm. in diameter, about 10 cm. long, foveolate, cortex more or less longitudinally cracked, forming elongate soralia, shorter and nearly circular above, soredia granular; ramuli 10–20 (–30) mm. long, very slender, infundibuliform at the base, annularly cracked just above, low-tuberculate and small-soraliate, tapering to an acute tip; summits capillaceous, distantly short-ramulose.

Cortex very fragile when dry, 115 μ thick, fastigiate, highly gelified; algal layer 65 μ thick, of discrete flattened colonies of *Trebouxia* 20–25 μ in diameter, separated by strands of closely woven medullary hyphae; medulla 300–350 μ thick, the outer 100 μ very compact, of predominantly periclinal hyphae, the inner portion of very loosely woven radial hyphae, occasionally dichotomous, 4–5 μ in diameter, very thick-walled, heavily nubilated with minute hyaline granules, arising as branches of dark brown periclinal hyphae, 6–7 μ in diameter; axis 360–400 μ in diameter, hyaline, of thick-walled longitudinal conglutinate hyphae.

The Socotra plant, referred here by Müller Argau, has a main axis about 2 mm. in diameter, is more clearly articulate with joints somewhat constricted at the ends and deeply foveate.

Mauritius: *Robillard*, portion of type com. Müller Argau, at Farlow Herb.
Socotra Island: *Schweinfurth*, com. Müller Argau, at Farlow Herb.

32. Usnea exasperata (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 440. 1937.

Usnea dasypogoides v. *exasperata* Müll. Arg., Flora 73:336. 1890.
Usnea dasypoga v. *exasperata* Zahlbr., Cat. Lich. Univ. 6:556. 1930.

Type: Tanganyika, Kilimanjaro, 3000 m. [3145 m., *fide* Stein in Meyer, Across E. African Glaciers, 353. 1891], *H. Meyer* in Genève; portion of same collection in Berlin, typical; another in Breslau, up to 60 cm. long, branches papillose and verruculose, probably an unnamed species.

Thallus 30–35 cm. long, pendent, flaccid, pale yellow when fresh, fawn to wood brown below, shading to vinaceous buff above, the ramuli and long capillaceous summits colonial buff to olive buff; holdfast a black verrucose disc giving rise to several axes, base 3–4 (–10) mm. long, about 0.8 mm. in diameter below, increasing to about 1.2 mm. in diameter just below the first branch, the lower third black, annulate; closely and somewhat unequally dichotomous in the lower 4 cm., with very short internodes, then very rarely dichotomous in the next 10–12 cm., about 1 mm. in diameter, tapering upward, then once or twice dichotomous at the bases of the very long, capillaceous summits; the larger branches subfoveolate, closely articulate, joints not or only very slightly inflated, axils somewhat complanate, very rarely ramulose; the upper portions of the main branches slightly obliquely rugose, the joints longer and the axils not complanate, the cortex sometimes subareolately cracked, the cracks white-margined, not verrucose nor papillate; ramuli 10–30 mm. long on the larger branches, perpendicular to the axis but variously curved and twisted, only 4–5 mm. long on the slender capillaceous portion of the thallus, with small low tubercules which probably develop minute isidiose soredia on most of the ramuli, although only a few have developed so far in our plants. Medulla K— or slowly yellow.

Apothecia (in *Hendrickx 4330*) 2–3 mm. in diameter, lateral on slender branches or large ramuli; exciple nearly plane, smooth or nearly so; marginal cilia subdistant, up to 10 mm. long, curved, annularly cracked at the base and sparingly so above, slender; disc carneous, white-pruinose.

Turrall 37 is sterile and quite sorediose, but apparently belongs here. The material from Kikuyu, Kenya, is only a fragment, the joints somewhat longer and more inflated, the tubercles on the smaller branches forming slightly elevated isidiose soralia. Some of the broken branches have regenerated dense clusters of short ramuli, about 3 mm. long.

KENYA: Kikuyu, *without collector, no. 39*; Elgon, *Miss R. J. Bush*, in E. Africa Herb. 10,573; Aberdares, *W. J. Dowson 293*, at Kew.

TANGANYIKA: Kilimanjaro, Marangu-Bismarck, 2140 m., *R. G. Turrall 37*; Bismarck Hill, 3220 m., *P. J. Greenway 3816*, at Kew.

CONGO: route Kahusi, 2450 m., on *Hagenia*, *F. L. Hendrickx 3679*; Mt. Kahusi, ca. 2700 m., *F. L. Hendrickx 4300, 4305, 4308, 4311, 4316, 4330*; all in E. African Herb.

33. Usnea Pinkertonii Stirton, Scottish Nat. 6:294. 1882.

Type: Egypt, Petrified Forest near Grand Cairo, *Pinkerton*, in the Art Galleries of the Glasgow Corporation.

Thallus 18 cm. long in type, over 25 cm. in our plants, pendent, flaccid, buffy brown on main axes to citrine drab on smaller branches; base blackened and rather hard in type, absent in our specimens, infrequently dichotomously or sympodially branched on the main axes, more closely so on the smaller branches; main axes up to 1 mm. in diameter, closely articulate, joints very slightly inflated, slightly rugulose and subfoveolate, some very minutely and acutely papillate especially in the

mid-portion of the thallus, others epapillate, backs of ridges often white-punctate (pseudocyphellae ?); ramuli irregularly disposed, sometimes quite close, sometimes absent for some distance on the main axes and secondary branches, usually close on the smaller branches, very slender, mostly 2–3 mm. long, some up to 7 mm.; summits capillaceous, very densely branched.

Apothecia lateral on secondary branches, up to 10 mm. in diameter, cupulate becoming nearly plane; exciple smooth in smaller apothecia, slightly rugulose and subpapillate on the larger ones; marginal cilia quite close, rather long, the longer often forked; disc dark carneous, white-pruinose at first, becoming nearly nude in age.

Although placed by Motyka in the BARBATAE, subsect. PENDULINAE, the olive fuscous color, the very thin cortex and thick lax medulla, the subarticulate thallus with rugose to subfoveolate joints all point to a close relationship to the STRAMINEAE subsect. SULCATAE, although papillae are very rare in the STRAMINEAE except in *U. straminea* Müll. Arg. *Bally 5611* seems to belong here. The specimen consists of the upper portion of a main axis and six secondary branches. No papillate joints were seen.

EGYPT: Petrified Forest near Grand Cairo, *Pinkerton*, in Art Galleries of the Glasgow Corporation.

ETHIOPIA: Galla Pass, 9° 28′ N., 42° 19′ E., 2520 m., *J. B. Gillett 5130*, Abyssinia-Somaliland Bound. Comm.; Simien, Mindigabsa, *H. Scott 323b*, sterile; both at Kew.

KENYA: Northern Frontier Province, 1560–1610 m., on *Cineraria grandiflora*, *P. R. O. Bally 5611*, at Kew.

34. USNEA CAMEROONENSIS Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Cameroons, *Miss Cheeseman L3*, at Kew.

Thallus pendent, rather flaccid, more than 55 cm. long, main axes drying snuff brown, Sayal brown to cinnamon, ramuli deep olive buff, base broken away; articulate, joints about 1.5 mm. in diameter below, mostly 1 mm. above, thinning gradually; closely several times dichotomous below, then unbranched for 10–20 cm., occasionally dichotomous above; axils subcomplanate, joints variable in length, many about 10 mm. long, constricted at the ends, usually showing the axis in the cracks, not or only very slightly inflated, longitudinally rugose, the ridges low, cracked at the top and farinose, flattened but not sulcate between; ramuli irregularly disposed throughout, up to 30 mm. long on the main axes, base subarticulate and inflated, tapering to a slender acute tip, about 10 mm. long on the secondary branches, surface low-tuberculate and deformed, forming isidiose soredia which soon break away causing the tops of the tubercles to appear farinose, somewhat in rows in the lower portions. Apothecia not seen.

Cortex 55 μ thick, fastigiate in a gel, outer 8–10 μ nubilated with minute brownish crystals; algal layer 30 (–40) μ thick, of densely packed protococcoid cells 6–8 μ in diameter; medulla 185–195 μ thick, of loosely woven thick-walled hyphae 3 μ in diameter, somewhat more compact next the algal layer; axis 250 μ

in diameter, of conglutinate, thick-walled hyphae 5–6 μ in diameter, lumen 3 μ and in the central portion a few large brownish hyphae 6–8 μ in diameter, nubilated with minute brownish crystals.

CAMEROONS: *Miss Cheeseman L3*, at Kew.

35. USNEA FUSCA Motyka, Lich. Gen. Usnea Stud. Monog. 473. 1937.

Type: S. Africa, Transvaal, Lydenburg, *Wilms*.

Thallus pendent, up to 20 cm. long (30 cm. in our material), green becoming buffy brown on the main axes, shading to honey yellow or chamois on the smaller branches; holdfast thin, circular, 2–3 mm. in diameter, darker but not black, base 1–2 mm. long, about 0.5 mm. in diameter, then dichotomous at right angles and the branches pendent from opposite sides of the branch of the tree, rarely dichotomous in the next 4–10 cm., then more frequently and more closely so near the summits, flexuous to nearly straight; main axes up to 1.5 mm. in diameter, articulate, joints variable in length, cylindric or very slightly inflated, not or only slightly constricted at the ends, nearly terete but somewhat deformed to obtusely angled, rugulose, the ridges oblong and mostly oblique, backs ecorticate and farinose, cortex sometimes cracked and subareolate; axils of larger branches flattened; ramuli almost absent below, more frequent above but perhaps only members of unequal dichotomies; summits long-capillaceous. Apothecia not seen. Soredia isidiose, becoming farinose from tubercles of the main axes, very small-punctate, not elevated on the smaller branches.

In the northern portion of its range, whence our material came, the species assumes more the habit of *U. exasperata*; cf. specimen from Kilimanjaro, *Uhlig*, cited by Motyka, loc. cit. 474.

KENYA: Chyulu Hills, *H. D. van Someren* (2 sheets in E. African Herb.).
UGANDA: Kigezi, Mafuga, 2580 m., *I. R. Dale L41*, fragments; Toro, Fort Portal, 1625 m., *I. R. Dale L40*, fragments tangled with other spp.; both at Kew.
TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., *P. J. Greenway 6532*, at Kew.
CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4314* (native name: *ndendu mushi*), in E. African Herb.

36. USNEA DECIPIENS Motyka, Lich. Gen. Usnea Stud. Monog. 477. 1937.

Type: Tanganyika, Mt. Msimbwa near Lake Tanganyika, 2300 m., corticole, *Münzner*.

Thallus pendent, somewhat rigid, over 40 cm. long, sepiaceous-fuscous (snuff brown on larger branches, Isabella color on small branches in our material), smooth, almost shining; base indistinct, 3 mm. long, 1 mm. in diameter, expanding to 2 mm. at first branch, not blackened in our material; main branches 2 mm. in diameter below, tapering very slowly, rarely and irregularly articulate, only slightly constricted, fractures indistinct, acutely angled or subterete with distinct longitudinal (rarely somewhat oblique) ridges, backs pale, very deeply foveate or impressed, with very rare pseudocyphellae between; ramuli close, large and small

intermingled, the smaller 5 mm. long, the larger almost as large as the branches, thick at the base, tapering above to obtuse tips, continuous or rarely slightly articulate, often arcuate and contorted ridges, closer and less regular; summits indistinct, of longer and denser ramuli.

Our Uganda material is rather fragmentary, tangled with *U. vesiculata,* both species glued to the herbarium sheet. The above description is taken in part from Motyka's monograph. Our material differs in having the main axes almost eramulose, the ramuli irregular on the secondary branches, sometimes quite close, in others rather scattered. Some of the ramuli have tubercles developing hemispheric isidiose soralia which appear farinose after the isidia are shed.

UGANDA: Elgon, Madangi, 3550 m., on heath trees in alpine meadow, *A. S. Thomas 607 p. p.*, at Kew.

KENYA: Mt. Kenya, Kinangop, Aberdare, 2840–2900 m., on trees, *P. Chandler 2278,* ex hb. Botanist Dept. Agr. Uganda, at Kew.

36a. Var. RHODESIANA Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Southern Rhodesia, Matopos District, top of high granite hill, 1610 m., on tree, *Frederick Eyles 1023,* at Kew.

Thallus pendent, subflaccid, over 30 cm. long (incomplete), Isabella color, ramuli somewhat lighter; base not seen; infrequently dichotomous, not articulate nor annulate, longitudinally and subreticulately rugose, ridges subacute, cortex often cracking along the ridges, subareolate and somewhat scaling, deeply foveolate or sulcate between the 6–10 ridges per circumference of transverse section, about 1 mm. in diameter, thinning to about 0.5 mm. in the upper 15 cm., but summits not capillaceous; ramuli close throughout, 3–15 mm. long, the longer perhaps arrested branches as they are sparsely and minutely ramulose or bear low tuberculiform, farinose soredia.

Cortex 40 μ thick, fastigiate, pseudoparenchyma cells 5–6 μ in diameter, nubilated with brownish crystals in the outer 15 μ; algal layer 30 μ thick, nearly continuous except in cortical cracks, cells protococcoid; medulla 30–40 μ thick, of densely woven mostly periclinal slender hyphae; axis 600–625 μ in diameter, slightly angled, of uniformly longitudinal, conglutinate thick-walled hyphae.

The cortex and medulla are proportionally much thinner than in *U. decipiens* and the ramuli closer and more sorediose.

37. USNEA AEQUATORIANA Motyka, Lich. Gen. Usnea Stud. Monog. 476. 1937.

Type: Uganda, Mt. Ruwenzori, 2900–3220 m., *Scott-Elliott.*

Thallus pendent, up to 60 cm. long, flaccid, main axes bister to snuff brown, ramuli and capillaceous summits buffy olive or lighter; holdfast black, about 3 mm. in diameter, an interwoven mass of root-like fibers penetrating the bark; base articulate, about 0.8 mm. in diameter below, rapidly expanding to 1 mm. or more, about 2 mm. long, then several times dichotomous forming several main axes, then very rarely dichotomous, about 1 mm. in diameter, slowly tapering to the long

capillaceous summits; articulate, joints not or very slightly inflated, slightly constricted at the ends in the larger branches, cylindric in the smaller branches; larger branches slightly but distinctly angled, ridges longitudinal, few, backs white-pruinose, rarely only slightly sulcate or foveolate, smaller branches smooth, terete, mostly ramulose; ramuli 4–5 mm. long, curved, bases thick, tips acute, rather dense but with sections of the principal axes almost eramulose. Soredia not seen.

Apothecia common, up to 10 mm. in diameter, mostly smaller, subterminal on lateral branches, exciple smooth except for 3–5 low, rounded, radiating ridges, a few of the larger apothecia subfoveate or impressed; marginal cilia dense, up to 10 mm. long, patent or recurved, thick, annulate; disc subconcave to almost plane or somewhat deformed, white-pruinose.

ETHIOPIA: without locality, *Schimper*, ex Herb. Sbarbaro sub *U. florida* v. *strigosa*, at Farlow Herb.

KENYA: Endabarrá, Mau forest, 2350 m., in *Acacia* grove at forest edge, *P. R. O. Bally B4947*; uplands, 2250 m., *E. R. V.*, ex Corydon Mus. Kenya 5161, at Kew; Mt. Elgon, 2790 m., *E. J. Lugard & Mrs. Cyril Lugard 490*, at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L. 43*; Imatong Mts., Mt. Kineti, *A. S. Thomas 1893*, both at Kew.

38. USNEA FLACCIDA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 475. 1937.

Usnea angulata v. *flaccida* Müll. Arg., Flora 73:337. 1890.

Type: Kenya, Leikipia at foot of Aberdare Mts., corticole, *L. von Hoehnel 176*.

Thallus pendent, flaccid, ca. 13 cm. long (Motyka), up to 30 cm. long in our material, becoming buffy brown on main axes, ramuli somewhat lighter; base about 1 cm. long, 0.5 mm. in diameter; articulate, joints cylindric, with short ramuli, not blackened; then closely dichotomous, axils flattened, then less frequently dichotomous throughout; flexuous, articulate, joints not inflated, up to 1 mm. in diameter below, thinning at each dichotomy but mostly about 0.5 mm. with long capillaceous summits; few elevated, acute ridges on the lower foveate joints, less ridged above, the upper joints almost cylindric, otherwise smooth; ramuli rather close, evenly distributed throughout, slender, 0.3–10 mm. long, somewhat curved.

Apothecia absent in the type and in our material. Motyka reports a specimen from Kilimanjaro, 3300 m., *Uhlig*, with apothecia up to 10 mm. in diameter, sublateral, thin, exciple plane or slightly concave, distinctly foveolate; marginal cilia few, slender, variable in length, flaccid; disc plane or slighly convex, often tuberculate-deformed; thecium 50 μ tall; ascospores 7 $\times$ 10 μ, ellipsoid, in narrow asci.

SUDAN: Imatong Mts., Mt. Kippia, pendent from twigs of trees in grassland, 2580 m., *A. S. Thomas 1823A*.

KENYA: Leikipià plateau and Aberdare Range, district around Nyeri, hanging from twigs, *W. Scoresby Routledge*, at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., on tree, *I. R. Dale L43*.

SOUTH AFRICA: Adelaide, *Miss D. K. Kingon*, com. Rev. W. Lilliè, in Howe Herb. sub *U. florida* v. *perplexans* (Stirton) Zahlbr. det. M. Bouly de Lesdain, at Farlow Herb.

39. Usnea terricola Dodge, Ann. Mo. Bot. Gard. 43:394. 1956.

Type: Cameroons, Mamoquilles, 2450 m., terricole among mosses and *Stereocaulon* sp., *Miss Cheeseman 25*, at Kew.

Thallus fruticose, subrigid, 8–10 cm. tall, cinnamon buff to buffy brown, irregularly black-maculate on the main axes, summits dark olive buff; base black, densely dichotomous at soil level, probably sending coarse root-like structures into the soil (broken off in collecting), rapidly expanding from 1 mm. to 2–3 mm. in diameter in the lower and middle joints, then tapering to 0.5 mm. in the ultimate joints; articulate, joints 5–20 (–30) mm. long, constricted at the ends, cracks varying from very narrow to 1 mm. wide, dichotomous throughout; basal joints nearly smooth with punctiform pseudocyphellae, and cortex cracked, forming low short ridges, sulfur-farinose, which may develop minute isidiose soredia; intermediate and upper joints more or less minutely verrucose with more abundant and elevated ridges, sometimes becoming reticulate and giving a foveate appearance, on the upper joint occasionally developing an apotheciform soralium covered with minute isidiose soredia, or part of the verrucae may form small elevated soralia. The soredia sometimes develop *in situ* producing dense clusters of pseudoramuli or becoming minute dichotomous thalli, joints only 0.3–0.5 (–1) mm. in diameter; summits obtuse.

Cortex 50 μ thick, loosely fastigiate in a gel, outer 20 μ nubilated with minute brown crystals; algal layer 35 μ thick, a continuous layer of densely packed protococcoid cells 8 μ in diameter; medulla 375 μ or more thick, of thick-walled hyphae 5–6 μ in diameter, very densely woven in the 50 μ next the algal layer, rest very lax, of predominantly radial hyphae; axis 300 μ in diameter, of conglutinate, longitudinal thick-walled hyphae, 3–4 μ in diameter.

cameroons: Mamoquilles, 2450 m., terricole, *Miss Cheeseman 25*, at Kew.

40. Usnea hispidula Motyka, Lich. Gen. Usnea Stud. Monogr. 488. 1937.
Usnea barbata v. *hispidula* Müll. Arg., Bot Jahrb. [Engler] 20:245. 1894.

Type: Tanganyika, Usambara, *Holst.*

Thallus about 15 cm. long, subpendent, quite rigid, fuscidulous in the herbarium, larger branches ochraceous tawny, ramuli dark olive buff, smooth; base absent in type, of rooting fibers penetrating bark at least 2 mm., not expanded into a holdfast, not blackened; primary branches 1.5–1.8 mm. in diameter, secondary branches thinner, constricted at the base, then slightly inflated and tapering gradually to the tips, continuous, or annularly cracked where the secondary branches leave the primary, smooth, with cylindric papillae (probably arrested ramuli); ramuli slender, 1–2 (–4) mm. long, minutely tuberculate and soraliate, forming all gradations between spinules and small tertiary branches; summits capillaceous, about 1 cm. long, tips acute, smooth or nearly so; soralia small, isidiose at first

becoming farinose, abundant on the smaller branches and the longer ramuli, rather rare on the larger branches.

UGANDA: Bugishu, Butandiga, 2130 m., arboricole, *A. S. Thomas 2565*, at Kew.
N. RHODESIA: East Isoka District, uplands, 1480 m., arboricole, *C. G. Trapnell*, a fragment lacking both base and summits, at Kew.

41. Usnea usambarensis Motyka, Lich. Gen. Usnea Stud. Monog. 489. 1937.

Type: Tanganyika, Usambara, Nguelo, *Kummer*.

Thallus up to 15 cm. long, pendent but quite rigid for its size, pale green when fresh, drying between deep olive buff and colonial buff; holdfast convex, about 2 mm. in diameter, not blackened; closely branched just above the holdfast, then less frequently dichotomous, branches nearly perpendicular, internodes variable in length, flexuous, about 1 mm. in diameter below to about 0.5 mm. above, summits mostly broken off, the few remaining about 2 cm. long, flexuous, tips obtuse, rather rigid, about 0.2 mm. in diameter; primary axis smooth, irregularly annulate and areolate, the areoles with raised margins; the middle portion rugose and low-angled, resembling *U. africana*; the upper portion, especially the smaller branches, low-tuberculate and deformed, the tubercles bearing a few rather coarse isidioid soredia, appearing farinose as the isidia break away, sometimes almost ecorticate in patches; ramuli subdistant, 2–3 mm. long, some longer, dichotomous, and resembling small lateral branches, flexuous, tapering from base to rather blunt tip, the shorter smooth, the larger minutely annulate and tuberculose, forming small soralia and eventually appearing decorticate.

Our plants from the Sudan are small, only about 5 cm. tall and only beginning to form soredia, probably juvenile. The plants from Madagascar are also small but quite punctate-sorediose above.

SUDAN: Onyiro, Issore, 1710 m., 32° 50′ E., 3° 50′ N., *T. F. Chipp 57*, at Kew.
MADAGASCAR: Imerina, Andragoloaka, *Hildebrandt*, ex Herb. Sbarbaro sub *U. dasypogoides* v. *sorediosula* Müll. Arg., at Farlow Herb.

42. Usnea cartilaginea Laurer in Motyka, Lich. Gen. Usnea Stud. Monog. 493. 1937.

Type: Cape of Good Hope, Table Mt., *J. F. Drège*.

Thallus 7–10 cm long, subpendent, quite flaccid, pale green, drying fuscous (Sayal brown to cinnamon), slender branches lighter; basal disc 2 mm. in diameter, base 1 mm. in diameter below, expanding rapidly to 2 mm. at the first branch, branching sympodial; branches articulate, joints inflated in the middle and constricted at the ends, not tapering upward, terete, smooth, with scattered minute tubercles below, closer above where they produce single small isidia; ramuli irregularly disposed and rare on the lower joints, more regularly subdistant above, straight, articulate, constricted at the base, inflated then tapering to a slender acute tip, indistinctly tuberculate, paler than the axes; summits more slender, less

conspicuously articulate, tips obtuse, more closely tuberculate, each tubercle producing an isidium, very rarely more. When the isidia are shed the remaining scars resemble minute white pseudocyphellae.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4316*; km. 30, route Kahusi, *F. L. Hendrickx 4322*; both in E. African Herb.

UGANDA: Mt. Elgon, 1290 m., arboricole, *W. Small 218*, at Kew.

SOUTH AFRICA: without locality, *Drège*, ex herb. W. Sonder, in Tuckerman herb. sub *U. florida*, at Farlow Herb.

43. USNEA TRANSVAALENSIS Vainio, Ann. Univ. Fenn. Aboens. $A2^3$:1. 1928.
Usnea pectinata Stirton, Scottish Nat. 7:77. 1883, non Taylor.
Usnea tropica Zahlbr., Cat. Lich. Univ. 6:596. 1930.
Usnea florida v. *densirostra* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1888/89: 145. 1890, excl. syn.

Type: Transvaal, Barbeton, saxicole, *P. A. van der Bijl 229*. The type of *U. pectinata* Stirton and *U. tropica* Zahlbr. is from S. Africa, Somerset East, *P. MacOwan*, in the Art Galleries of the Glasgow Corporation.

Thallus erect, fruticose, rigid, 3.5–5 cm. tall, pale green, becoming old gold to Isabella color; holdfast up to 4 mm. in diameter, of black, branched and tangled rootlets, formed by a coalescence of several plants or branching at the very base; primary axes 1–1.5 mm. in diameter, 2–6 mm. long to the first branch, not blackened, then closely dichotomous, almost at right angles, the branches curving upward; branches rare in the upper half, slightly constricted and annularly cracked at the base, about 0.8 mm. in diameter below, tapering upward to blunt tips; sparingly annularly cracked throughout, terete, glabrous below, appearing minutely verrucose above from the initials of soralia; ramuli very dense, mostly about 1 mm. long, a few up to 2 mm., tips blunt, very minutely verrucose but mostly covered with minute soralia of isidiose soredia which often germinate *in situ*, forming small isidia 0.1–0.2 mm. long, with blackened tips, and thus appearing secondarily ramulose; apothecia not seen.

Cortex 80 μ thick, fastigiate, highly gelified, the outer 10 μ with minute brownish crystals; algal layer 30 (–40) μ thick, continuous, cells protococcoid, 11–12 μ in diameter, somewhat polyhedral from mutual pressure; medulla 270 μ thick, of very loosely woven hyphae 3–4 μ in diameter, lumen about 1 μ, somewhat nubilated with hyaline granules; axis solid, 150 μ in diameter, of slender thick-walled, predominantly longitudinal hyphae.

The relationship of this species to *U. pulvinata* Fr., collected by Preiss in Western Australia, is not clear. Motyka's description is based on the whole complex from South Africa northward to Kenya. He states that the medulla is evanescently K yellow, while in the type of *U. transvaalensis* and in our material, the medulla is K yellow becoming red and finally reddish fuscous. He states that the ramuli are intermixed, short and long, up to 10 mm., not cracked at the base, and tips

subulate, often blackened; while in our material the ramuli are nearly uniformly 1 mm. long, with very few reaching 2 mm. In our plants the cortex is thicker and the algal layer and medulla are twice the thickness of the axis, while in *U. pulvinata* (*fide* Motyka) the cortex is thinner and the medulla only three fourths as thick as the axis.

UGANDA: Karamoja, Napak, 2250 m., on rocks in mountain grassland, *A. S. Thomas 3631*; Imatong Mts. 2100 m., *A. S. Thomas 1678*, both at Kew.

SOUTH AFRICA: Somerset East, *P. MacOwan*, type of *U. pectinata* Stirton non Tayl. and *U. tropica* Zahlbr., in the Art Galleries of the Glasgow Corporation.

MADAGASCAR: Imerina, Andrangoloaka, saxicole, *Hildebrandt 2172*; Prov. Betafo, *native collector*, ex Herb. E. G. Paris; both at Farlow Herb.

44. USNEA RUWENZORIANA Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belg. 5:27. 1936.

Type: Congo, Mt. Ruwenzori, 4000 m., ramicole, *L. Hauman 929, 947*.

Thallus erect, 4 cm. tall, cespitose, pale ashy green, drying dirty fuscous (Saccardo's umber to light brownish olive in our plants); base hemispheric, 1.5 mm. in diameter, narrowing to 0.3–0.6 mm., 1–3 mm. to the first dichotomy, lower portion blackened; closely several times dichotomous near the base, axils 45–90°, main branches 1–1.2 mm. in diameter below, tapering gradually to short abrupt summits, terete, smooth, dull, rarely somewhat foveolate; ramuli quite dense, mostly about 2 mm. long, quite slender, slightly constricted at the base and somewhat inflated in the middle, some growing out as secondary branches; tubercles on summits and upper ramuli forming soralia, isidiose at first, soon eroded and farinose.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., arboricole, *I. R. Dale L43*; Bugishu, Butandiga, 2410 m., *A. S. Thomas 484* (slightly lighter in color, younger?); both at Kew.

TANGANYIKA: Kilimanjaro, 2900–2916 m., *R. G. Turrall 55*, at Kew.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4300*, in E. African Herb.

45. USNEA HAUMANII Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belge 5:25. 1936.

Type: Congo, Mt. Ruwenzori, southwest slope, 4200 m., on *Senecio Friesorum* and *Helichrysum Stuhlmannii*, *L. Hauman 921*.

Thallus pendent, flaccid, up to 10 cm. long, pale ashy green, (larger branches tawny olive in our much older material), constricted at the base, then expanding rapidly to 1.5 (–2) mm. in diameter, irregularly dichotomous throughout, axils varying from 45 to 90°, irregularly curved, branches somewhat constricted at the base, rather thick throughout, irregularly annularly cracked, nearly terete, surface smooth or slightly rough from low tubercles (initials of small soralia?); ramuli very rare or absent, the few present suggesting that they are young branches arising from unequal dichotomy; summits indistinct.

Apothecia not seen. Soralia abundant on the slenderer branches, up to 0.2 mm. in diameter, sometimes crowded but rarely confluent, much smaller and more

scattered on the larger branches, subhemispheric, probably isidiose at first but mostly appearing farinose, some isidia germinating *in situ* and forming nest of propagula which early break away.

Our material from Cameroons consists of somewhat smaller plants, base broken away in collecting, color of the main branches darker (as they have been 23 years in the herbarium instead of 4 years at the time Motyka studied the type). Our plants were growing on stones, as were those from Kilimanjaro, 3500–4000 m., *Fr. & R. Wettstein,* cited by Motyka in his original description. The Uganda material is more typical. The Angola material is just beginning to form apothecia, sessile on the main axes for some distance back of the ultimate branches.

CAMEROONS: Mt. Cameroon, 4030 m., on bare rocky ground, *F. W. H. Migeod 196,* at Kew.

UGANDA: Kigezi, Muhavura, 3610 m., saxicole, *I. R. Dale L18,* at Kew.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo-Cuvo River, 1000 m., on dead trees, *J. Gossweiler 9991a,* at Kew.

46. USNEA SIMPLICISSIMA Motyka in Zahlbr. & Hauman, Mém. Inst. Roy. Colon. Belge 5:29. 1936.

Type: Congo, Mt. Ruwenzori, 4000 m., on *Hypericum, L. Hauman 952.*

Thallus 5 cm. or less tall, simple or sparingly branched, subfruticose, pale green when fresh, drying between buckthorn brown and Dresden brown, opaque; base gradually but distinctly attenuate and blackened, several plants from a common holdfast giving a branched appearance; branches usually simple, somewhat curved, thickened to 1.3 mm. in diameter, subinflated, tapering from the middle upward, continuous or rarely articulate, constricted in the cracks, terete to slightly compressed and deformed, quite closely ramulose; ramuli 5–15 mm. long, variously curved, slightly tuberculate, tips rather obtuse.

Apothecia apical, up to 5 mm. in diameter, often subirregular; exciple smooth, subconvex; marginal cilia relatively abundant, erect at first, finally spreading, of variable length; disc concave at first, becoming nearly plane, carneous, white-pruinose; ascospores 9–11 μ in narrow asci.

Cortex about 30 μ thick, papery; medulla about 200 μ thick, very lax, white; axis 180 μ in diameter.

Our material from the Buddu District is evidently quite young, 2 (–3) cm. tall, the taller mostly once-dichotomous near the middle; apothecia cupulate with erect marginal cilia, only about 1 mm. in diameter, lateral near the tip, not strictly apical. Except for smaller dimensions, our plants agree quite well with Motyka's description translated above.

UGANDA: Buddu District, on twigs in sandy plain, 3950 [m. or ft.?], *H. U. Baul* [surname rather illegible], ex Bot. Gard. Entebbe, 1905; Kigezi, Kasatoro, in forest, 1930–2580 m., *I. R. Dale L39 p. p. min.*; both at Kew.

47. Usnea fuscorubens Motyka, Lich. Gen. Usnea Stud. Monog. 546. 1937.

Type: Mauritius, without locality, *Simony*.

Thallus 6 cm. long, evidently subpendent, main axes Mars brown, secondary branches and ramuli russet; irregularly dichotomous throughout, axils about 90° angles; branches 1–1.5 mm. in diameter, irregularly curved, almost terete, sometimes deeply foveate, continuous or sometimes annularly cracked, verruculose-papillate, papillae short, cylindric, esorediose; ramuli distant, variously curved and branched, very slightly attenuate at the base, subinflated, almost smooth, the larger subtuberculate and subfoveolate, tips acute.

Apothecia about 6 mm. in diameter; exciple smooth, shining, the larger ones minutely papillate and foveolate; marginal cilia up to 10 mm. long, often branched, similar to the ramuli; disc slightly concave, densely white-pruinose.

The specimens from the Cape of Good Hope are somewhat larger, one about 7 cm. long, the other 12 cm. long, the lower joints about 2 mm. in diameter, and the apothecia of the shorter plant 8–9 mm. in diameter; in other characters, both macroscopic and microscopic, they agree well with Motyka's description translated above.

south africa: Cape of Good Hope, without locality or collector, ex herb. Menzies in Tuckerman herb. sub *U. florida*, at Farlow Herb.

48. Usnea submollis Steiner, Verhandl. Zool. Bot. Ges. Wien 53:229. 1903.

Type: Cameroons, Fako, *Bornmüller*.

Thallus up to 5 cm. tall, simple or branched below, olive green (olive lake to ecru olive in our plants); holdfast indistinct, base not blackened, somewhat attenuate below, expanding to 0.6 mm. at the first branch; branching sympodial just above the base, branches somewhat constricted and annularly cracked at the base, inflated to 0.6 mm. in diameter in the lower third, then tapering to the tip; terete, not articulate, smooth or minutely and sparsely verruculose; ramuli not dense, about 1 mm. long, nearly perpendicular to the axis, bases articulate and slightly constricted, straight or slightly curved upward, slightly inflated, a few longer, up to 5 mm. long, with an occasional ramulus, perhaps aborted secondary branches; summits subulate.

Apothecia subterminal or lateral, sessile, 1.5 mm. in diameter, concave, exciple smooth; marginal cilia few (about 8), distant, suberect, resembling the small ramuli in size and shape; disc pale flesh color, white-pruinose.

Our Cameroons plants may be still immature as the dimensions are somewhat smaller than given by Motyka; the disc is covered by a white pruina. Our Nyasaland plants are a little larger than the type, the ramuli denser, and the apothecia up to 3 mm. in diameter.

cameroons: Buea, 1290 m., on sticks on the ground, *F. W. H. Migeod 22*, at Kew.
congo: Mt. Minagongo, *D. H. Linder 2172*, at the Farlow Herb. and in Mo. Bot. Gard. Herb.

NYASALAND: Mlange District, Luchenya Plateau, Mt. Mlange, 1890 m., at forest edge, *L. J. Brass 16828, 16847* (Vernay Nyasaland Exp.), at N. Y. Bot. Gard. and Mo. Bot. Gard. Herbs.

SOUTH AFRICA: Cape of Good Hope, summit of mountain above Simon's Town on Simon's Bay, *Charles Wright* (Rogers & Ringgold N. Pacific Expl. Exp.), det. *U. barbata* v. *florida* by Tuckerman ex Gray Herb., at Farlow Herb.

49. USNEA BLEPHAROIDES Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Tanganyika, Kilimanjaro, at upper limit of forest, 3000 m., *G. Geilinger 4417*, at Kew.

Thallus fruticose, little-branched, prostrate or suberect, about 9 cm. long, axes drying tawny olive, ramuli and cilia cinnamon buff; holdfast broken off, subarticulate, lowest joint slender, tapering upward, more than 3 mm. long, 1 mm. in diameter below, expanding to 2 mm. above; joints constricted but cortex mostly continuous, with usually two lateral branches on the outer side of the curve of each joint, producing flexuous main branches, the last 3 mm. of the axes and all lateral branches unbranched, or with 1–2 secondary branches scarcely larger than ramuli but bearing minute apothecia; main branches 2 mm. in diameter below, tapering to 1 mm. under the apothecia, terete (somewhat crushed in the type), slightly verrucose (visible under 12× magnification), becoming minutely papillate on the joints just below the apothecia and at the bases of the larger ramuli; ramuli subdistant, 4–5 (–10) mm. long, curving upward, articulate and subinflated at the base, tips acuminate.

Apothecia 11–12 mm. in diameter, sessile on axes and slender branches, about 1.5 mm. from the tip, appearing terminal when mature, with concrescent ramuli forming low radial ridges, minutely verrucose (under 12× magnification); marginal cilia distant, up to 10 mm. long, curved, tips acuminate; disc flat, flesh color with a thin white pruina.

Cortex 85–125 μ, very variable in thickness, forming verrucae outside up to 60 μ tall and protruding as teeth between the algal colonies, 60 μ toward the medulla, outer 55 μ fastigiate, of conglutinate thick-walled hyphae 8 μ in diameter, lumen 2 μ, the rest of densely woven, predominantly periclinal thick-walled conglutinate hyphae, but the teeth between the algal colonies of radial hyphae, the outermost 15 μ nubilated with minute brown crystals; algal layer discontinuous, colonies about 30 μ in diameter, cells of *Trebouxia* 6–7 μ in diameter, closely packed; medulla about 375 μ thick, the outer portion (about 80 μ) densely woven, the rest of very loosely woven, predominantly radial hyphae 8 μ in diameter, lumen 3 μ, dichotomously branched; axis 250 μ in diameter, of longitudinal conglutinate thick-walled hyphae 3 μ in diameter.

This species differs from *U. blepharea* Motyka in having a larger axis, more gradually attenuated upper portions of the branches, fewer ramuli, an exciple without spinules, and a more regular disc. Perhaps the specimen from Kilimanjaro cited by Motyka belongs here rather than in *U. blepharea,* which is otherwise a Javan and Bornean species. Perhaps a single plant sorted out of *R. G. Turrall 55*

may also be this species. It is only 4 cm. tall, about 1 mm. in diameter below, surface not quite as verrucose and apothecium only 3.5 mm. in diameter.

TANGANYIKA: Kilimanjaro, at upper limit of forest, 3000 m., *G. Geilinger 4417*, type; 2930–3045 m., on twigs of giant heather in clearing in forest, *R. G. Turrall 55 p. p. min.*; both at Kew.

50. USNEA MOLLIUSCULA Stirton, Scottish Nat. 7:77. 1883.

Type: Australia, Victoria, subalpine country in upper Ovans River, *Mrs. McCann 1*, in Art Galleries of the Glasgow Corporation.

Thallus 6–7 cm. tall, fruticose, subflaccid, ochraceous tawny to buckthorn brown; holdfast about 3 mm. in diameter, of rootlike strands, dark, giving rise to 2–3 axes up to 2.3 mm. in diameter, somewhat attenuate but not blackened at the base; branching unequally dichotomous to sympodial, articulate, lowest joint nearly cylindric, about 5 mm. long, smooth, upper joints inflated, tuberculate to subpapillate, many papillae growing out as short, rather coarse spinules, sometimes in rows in the upper joints just under the apothecia, giving a somewhat foveolate appearance; ramuli sparse in the type, mostly 1–3 mm. long, a few up to 10 mm., annularly cracked and slightly inflated at the base.

Apothecia sessile, about 8 mm. in diameter, margins somewhat inrolled when dry; exciple smooth or somewhat reticulate-foveate; marginal cilia distant to irregularly close, very variable in length, up to 5 mm. long, tips acute, mostly broken off; disc white-pruinose; ascospores 9–11 $\times$ 7–8 μ.

In our South African material, the ramuli are irregularly dense, 2–3 (–10) mm. long, the longer annularly cracked in the middle and sparingly again ramulose. The apothecia are subterminal on short lateral branches, the exciple is smooth, the marginal cilia closer, shorter, and more inflated.

AUSTRALIA: Victoria, subalpine country of upper Ovans River, *Mrs. McCann 1*, in the Art Galleries of the Glasgow Corporation, a fragment in the British Museum.

CONGO: Mt. Kahusi, 2700 m., ramulicole, *F. L. Hendrickx 4308, 4314*, both in E. African Herb.

SOUTH AFRICA: Hermansdorp, Blue Lilies Bush, corticole, *A. Woodcock*, at Kew.

51. USNEA OBTUSATA Motyka, Lich. Gen. Usnea Stud. Monog. 622. 1938.

Type: Ethiopia, north slope of Mt. Kubbi, *Schimper*.

Thallus up to 8 cm. tall, fruticose, subrigid, dirty ashy greenish in herbarium (Motyka) but sepia shading to tawny olive in our material; base black, about 1 mm. in diameter, main axis rapidly expanding to 2 mm. and tapering upward to 1.5 mm. just below the terminal apothecium; lateral branches about 1 mm. in diameter, nearly perpendicular to the main axis but curving upward, subarticulate, slightly inflated, smooth or irregularly papillate (evidently very young ramuli); ramuli dense, perpendicular, mostly 1–2 mm. long, sometimes in longitudinal rows in the upper portion, giving a subrugose appearance, tapering from the base to a blunt tip, not articulate nor inflated, slightly curved upward.

Apothecia terminal (really subterminal, the tip of the branch concrescent with the exciple and protruding about 3 mm.); exciple smooth, with spines about 1 mm. long; marginal cilia close, about 3 mm. long, straight or slightly incurved, tapering to an acute tip, rather fragile; disc concave to somewhat deformed and coarsely rugose, flesh color (Motyka), tawny olive or darker in our material, white-pruinose.

Cortex 40–50 μ thick, of fastigiate pseudoparenchyma, thick-walled conglutinate cells, lumina 5–6 μ in diameter; algal layer 100 μ thick, cells densely packed under the cortex and next the medulla, more scattered between, protococcoid; medulla 300–360 μ thick, of very loosely woven, thin-walled hyphae 3–5 μ in diameter; axis solid, 160 μ in diameter, of vertical, thick-walled hyphae 2.5–3 μ in diameter.

51a. f. PERSTRIGOSA Motyka, Webbia 8:391. 1952.

Our material probably should be referred to f. *perstrigosa* Motyka, differing in strict, more acute ramuli, often very dense and paler fuscous The species was originally placed in the ALBOMACULATAE, but transferred by Motyka (*loc. cit.*) to the SETULOSAE, DENSIROSTRES. Although the original description calls for "sordide cinereo-viridulus," the description of the variety implies that the species is fuscous. Pseudocyphellae are not mentioned in the original description, hence the species does not belong in the ALBOMACULATAE. The thick, lax medulla, fuscous color in the herbarium, lack of papillae, and denser ramuli indicate a place in the GLABRATAE, CILIIFERAE, perhaps near *U. simplicissima,* rather than in SETULOSAE, DENSIROSTRES, with their thinner, very dense medulla and grayish green colors. Unfortunately I have not seen Motyka's types. The axis is relatively thinner than the dimension given by Motyka.

ETHIOPIA: Mulu, 20 miles north of Addis Ababa, 2580 m., P. R. O. *Bally 2078,* at Kew; Bagla, 2410 m., *Hildebrandt,* 1872, ex Herb. Sbarbaro, at Farlow Herb.

51b. f. PERFLAVA Motyka, Webbia 8:392. 1952.

Type: Ethiopia, Bacino del Tana, 2100–2200 m., *Pichi-Sermolli.*

Differs from the type in its yellowish fuscous color, especially in the upper part of the branches with golden yellow ramuli.

Chipp 57, from southern Sudan, seems to belong here. The main axis is tawny olive, the lateral branches shading to chamois and the ramuli colonial buff. The main axis is articulate, the joints more constricted at the ends; the apothecia are somewhat smaller, the marginal cilia less dense, and some of the longer ones branched.

SUDAN: Onyiro, Issare, 1770 m., 32° 50′ E., 3° 50′ N., *T. F. Chipp 57,* at Kew.

52. USNEA UNDULATA Stirton, Scottish Nat. 6:104. 1881, *non alio loco.*

Usnea foveolata Stirton, Scottish Nat. 7:77. 1883.

Usnea barbata v. *farinosa* Müll. Arg., Flora 74:373. 1891.

Usnea farinosa Zahlbr., Cat. Lich. Univ. 6:564. 1930.

Usnea Steineri v. *tincta* f. *sorediosa* Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.

Type: Bechuanaland, West Griqualand, Kimberley, *J. Shaw*, in Art Galleries of the Glasgow Corporation. Type of *U. foveolata* from same locality and collector in British Museum (Natural History). Type of *U. barbata* v. *farinosa* and *U. farinosa* from South Africa, *Peter MacOwan.*

Thallus 9 cm. or more long (up to 30 cm., *fide* Stirton), fruticose, pale ashy green, becoming buffy olive in the herbarium; holdfast of discrete, branched, flattened rootlets, not united into a disc, about 3 mm. long, rose color below where torn from the bark, buffy olive above; several times dichotomous just above the base, axils nearly 90° angles, the branches 1.5 mm. in diameter, curving and soon nearly parallel, flexuous and undulate, internodes longer above, rather densely covered with short ramuli, about 1 mm. long below, shorter and more slender spinules above; the more slender branches somewhat foveolate from minute isidiose soredia in rows, forming very slight anastomosing ridges (perhaps only scars of broken-off spinules); summits indistinct, mostly broken off.

Apothecia (absent in our plants) about 7 mm. in diameter, subterminal; exciple smooth or foveolate, with short spinules; marginal cilia very few, short, subulate; disc plane, white-pruinose; ascospores 4×8 μ, in narrow asci (*fide* Motyka).

A somewhat variable species, extending from Kenya to South Africa. Material from Kenya seems to be shorter with more spreading branches, some discolored reddish (about cameo brown), probably from too slow drying in the plant press. Ridges and foveolation are very indistinct in most of the plants, but are much more distinct in the type of *U. foveolata* and in *Dale 43* from Uganda.

KENYA: Chyulu Hills, *H. D. van Someren* (2 sheets in E. African Herb.); Lake Ngunga, 1775 m., on trees, *G. M. Allen 1838*, in Howe Herb. sub *U. florida* v. *strigosa* at Farlow Herb.; Nairobi, on trees, *G. M. Allen 1784*, in Howe Herb. sub *U. florida* v. *strigosa* at Farlow Herb.; Mt. Kenya, 3000 m., *Edgar A. Mearns 1776* (T. Roosevelt Exp.), ex herb. G. K. Merrill at Farlow Herb.

COMORO ISLANDS: Johanna Island, Pomoni lowland, on *Cocos* trunks, *Hildebrandt*, ex herb. Sbarbaro sub *U. barbata* f. *sorediata*, at Farlow Herb.

UGANDA: Kigezi, Kasatoro, Kabale R., 2250 m., arboricole, *I. R. Dale L43*.

CONGO: km. 30, route Kahusi, *F. L. Hendrickx 4330;* Mt. Kahusi, ca. 2700 m., *F. L. Hendrickx 4142, 4303, 4307, 4316*; all in E. African Herb.

NORTHERN RHODESIA: uplands of E. Isoka District, 1480 m., on tree in *Brachystegia mimosaefolia* scrub woodland, *C. G. Trapnell*, in E. African Herb.

BECHUANALAND: W. Griqualand, Kimberley, *J. Shaw*, in Art Galleries of the Glasgow Corporation, type of *U. foveolata*; same locality and collector, in British Mus. (Nat. Hist.).

SOUTH AFRICA: Cape of Good Hope, Uitenhage, forest near Zunday's River, *Zeyher*, in Taylor herb. sub *U. florida*, Ach., *a state?*, at Farlow Herb.

53. USNEA STRIGOSELLA Steiner, Bull. Herb. Boissier, II. 7:637. 1907.

Type: South Africa, Transvaal, Letaba District, Mt. Mamotsuri, *Henri A. Junod;* terminal fragment in Howe herb. at Farlow Herb.

Thallus pendent, about 30 cm. long, 0.6–1 mm. in diameter, slender, greenish stramineous, drying mikado brown or lighter on the main branches, ramuli and smaller branches cream buff; base short (absent in our plants), several times closely dichotomous below, axils acute, and again several times dichotomous with longer

internodes above, axils nearly right angles; spinulose and closely ramulose, terete, annularly cracked, sometimes slightly constricted at the cracks, sometimes not; smooth at first, often becoming spinulose and the surface uneven from the scars of the fallen spinules, sometimes slightly deformed where the spinules and small ramuli are arranged in close rows but not angular; ramuli close to dense, mostly about 2 mm. long, a few longer; summits short and indistinct.

Apothecia rare (absent in our plants), about 6 mm. in diameter, sublateral; exciple nearly plane, smooth; marginal cilia dense, radiating, of variable length, up to 12 mm. long, often annularly cracked; disc nearly plane, pale sulfur pruinose; ascospores 4 $\times$ 8 μ in narrow asci.

Cortex 65–100 (–115) μ thick, fastigiate, gelified, yellowish brown from minute crystals in the outer 65 μ, more hyaline within; algae in discrete colonies, about 30 μ in diameter, with smaller colonies scattered in the medulla; medulla variable, 65–190 μ thick, thicker where the cortex is thinner, rather compact except in a narrow zone next the axis where it mostly tears apart in sectioning, hyphae 6–7 μ in diameter, nubilated with granules, hyaline in outer portion, brownish in inner 30 μ next the axis; axis about 420 μ in diameter, transverse section somewhat irregular, of conglutinate, longitudinal hyphae 3 μ in diameter, with scattered cavities 7–8 μ in diameter, filled with brownish crystals and surrounded by a layer of thin-walled hyphae (reminding one of the resin canals of conifers).

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16847* (Vernay Nyasaland Exp.) in N. Y. Bot. Gard. Herb.

SOUTH AFRICA: Transvaal, Letaba District, Mt. Mamotsuri, *Henri A. Junod*, type fragment, com. Zahlbruckner, in Howe herb. at Farlow Herb.

54. USNEA PERSPINOSA Motyka, Lich. Gen. Usnea Stud. Monog. 2:533. 1937.

Type: Cameroons, mountain forest, 2200 m., *C. Ledermann*.

Thallus about 5 cm. tall, fruticose, spreading, rigid, green when fresh, drying fuscous (Isabella color to light brownish olive in our plants), ramuli lighter; holdfast low, conic, verrucose, not blackened, 4 mm. in diameter, base about 2 mm. long and wide and densely sympodially branched at the top, then less closely, but internodes short throughout; axils nearly right angles, main axis 2 mm. in diameter below, tapering to about 1 mm. below the apothecia; branches constricted at the base and often articulate, 1–1.5 mm. in diameter, terete, smooth to somewhat rugose from rows of spinules, in places appearing short-papillate from healing scars of the caducous spinules which are about 0.2 mm. long; cortex areolate, diffract in some places; ramuli up to 3 mm. long, annularly cracked at the base, slightly inflated and surface uneven, tips acute, often broken off.

Apothecia abundant, subterminal, sessile, cupulate, 2–3 (–10) mm. in diameter; exciple subfoveolate, densely spinulose; marginal cilia very dense, erect, inflated, up to 3 mm. long, tips forked, acute; disc very concave, white-pruinose.

The Uganda plants are somewhat variable; *Dale L69* is larger, nearly 7 cm. tall,

less densely branched, with one apothecium about 6 mm. in diameter; *Dale L. 85* has a few apothecia up to 10 mm. in diameter; *Dale L38* consists of plants smaller in all dimensions; *Dale L41 p. p.* has large apothecia but is shorter. The Kenya plants are paler and less densely branched, and the marginal cilia of the apothecia are shorter and more spreading. However, they seem closer to this species than to any other. *Mearns 508* has apothecia up to 18 mm. in diameter.

CAMEROONS: Cameroon Mt. above Buea, 2500 m., on dead decorticate shrub in grassland, *J. Milbraed 10838,* sterile and juvenile.

UGANDA: Bunyoro, Busingoro, on bark of Jacaranda tree, *I. R. Dale L69*; Kigezi, Mafuga, 2410 m., on trees, *I. R. Dale L41 p. p.*; Kasatoro, Kabale River, 2250 m., on trees, *I. R. Dale L43*; Kabale, 2000 m., on bush of *Hibiscus rosa-sinensis, I. R. Dale L55*; Fort Portal, on *Eucalyptus,* 1620 m., *I. R. Dale L38*; Fort Portal District, Toro, on trees, *I. R. Dale L40;* Mt. Elgon, 1290 m., *W. Small 217*; Bugishu, Bulambuli, on trees, *A. S. Thomas 548,* very young, all at Kew.

KENYA: Ngong, *H. D. van Someren 1948,* in E. African Herb.; Guaso Nyiro, *G. M. Allen 1792,* in Howe herb. sub *U. florida* v. *strigosa* Ach.; Narok River, 2000 m., *Edgar A. Mearns 508* (Theodore Roosevelt Exp.); both at Farlow Herb.

55. USNEA LUTEOLA Motyka, Frag. Florist. Geobot. 1:33. 1954.

Type: Madagascar, Manakambahiny Est, Marovato between Alaatra and Marovato, 800 m., com. des Abbayes.

Thallus up to 8 cm. long (5.5 cm. in our plants), caespitose, fruticose, subflaccid, pale yellowish to yellowish stramineous (axis Sayal brown, slender branches and ramuli chamois in our plants); holdfast of radiating, rather large, dichotomous, white rootlets, adhering to the bark and penetrating it at their tips; base not blackened, 1.2 mm. in diameter, 14 mm. long; about thrice dichotomous with relatively short internodes, axils nearly right angles but curving upward, divergent, not parallel; terete, rather densely covered with ramuli about 3 mm. long, and slender lateral branches up to 15 mm. long; cortex continuous or cracked but not articulate, the fertile branches tapering to about 0.5 mm. in diameter below the apothecia, sterile branches tapering to long-acuminate summits; main axes smooth except for small verrucae which develop to ramuli, the more slender branches papillate and tuberculate, the tubercles producing soralia with very few isidiose soredia, becoming farinose after the soredia are shed; ramuli rather dense, about 3 mm. long, with acute tips on the main axes and lower portions of the slender branches, mixed with coarser ones up to 10 mm. long (perhaps better considered as young lateral branches as they are tuberculate-sorediose); summits about 1 cm. long, tuberculate-sorediose, usually eramulose, sometimes forked above, tips acute.

Apothecia lateral, about 1 cm. below the tips of the branches, bending them downward, so that the apothecia appear subterminal, 3–5 mm. in diameter, nearly plane; exciple smooth; marginal cilia 2-ranked, the outer row subdistant, up to 10 mm. long, tuberculate-sorediate, the inner row short, 0.5–1 mm. long, closer; disc flesh color, covered by a dense white pruina at first, somewhat rugose.

MAURITIUS: Reduit, corticole, *G. Orian 3,* at Kew.

56. Usnea sulphurascens Motyka, Frag. Florist. Geobot. 1:34. 1954.

Type: Madagascar, Manakambahiny Est, between Alaatra and Tanatave, 800 m., com. H. des Abbayes.

Thallus subdependent, flaccid, about 9 cm. long, sulfur yellow becoming ochraceous buff; base short, attenuate, indistinctly blackened; dichotomous to sympodially branched, axils nearly right angles, branches slightly constricted at the base, articulate, arcuate, axes 1–2 mm. in diameter, joints inflated in the middle, gradually tapering to the next articulation, terete, minutely tuberculate, tubercles bearing single white isidia and appearing pseudocyphelliform after the isidia are shed; summits slender, acuminate; apothecia not seen.

Cortex up to 40 μ thick, of coarse radial hyphae in a gel; algal layer 25–35 μ thick, cells *Trebouxia ?, 6–7* μ in diameter in discrete colonies, forming a nearly continuous layer; medulla 125–150 μ thick, very compactly woven just under the algal layer, then very lax, of relatively thin-walled, branched hyphae, mostly 5–6 μ in diameter.

Our plant is ochraceous buff instead of stramineo-ochraceous, perhaps from having been much longer in the herbarium; the branching is more dichotomous on the larger axes; otherwise it agrees well with Motyka's description. Our plant is only 5 cm. long, but the lower portion has been broken off.

MADAGASCAR: without locality, *Dr. Moss,* March 1895, at Kew.

57. Usnea syriaca Motyka, Lich. Gen. Usnea Stud. Monog. 278. 1936.

Type: North Syria, Amanus near Beiland, on *Abies* at foot of Akma Dagh, 2600 m., *Kotschy.*

Thallus about 10 cm. long, fruticose, rather slender, pale ashy green, slightly fuscent in the herbarium, darker on the primary branches (main axes mikado brown, slender branches and ramuli cinnamon buff in our plant), opaque, base short, rather rigid, dark, infrequently branched from the base, axils nearly 90° angles or more acute; branches somewhat flexuous, about 1 mm. in diameter near the base, tapering gradually upward, terete, continuous or rarely simply annulate, the thicker branches shortly and densely papillate, the more slender branches less so, forming very obtuse ridges, the backs decorticate and farinose, evidently producing soredia as well as the tips of some papillae; ramuli not close, mixed longer and shorter, very thick at the base, tapering gradually upward; summits rather long, farinose, so that they appear whitish.

Cortex 60 μ thick, rather hard and elastic, pale; medulla about 150 μ thick, white, dense, K intensely reddening; axis 330 μ in diameter with some dark hyphae.

Our plant from Eritrea agrees more closely with Motyka's description translated above than with any other, but the medulla is K—. The base is absent and the axis blackened about 2 cm. and up the secondary branches, suggesting that it is prostrate and the axis covered with leaf mold, in which case it may be much longer and the portion collected only the terminal portion. The cortex regenerat-

ing in the annular cracks shows as white rings about the lower portions of the secondary branches. The soralia are well developed, slightly elevated, producing granular soredia, in some places so crowded as to form almost continuous areas. The proportions of cortex, medulla and axis are nearly the same, but the absolute dimensions are nearly double. The structure of the cortex is unusual, being formed of interwoven and anastomosing hyphae with moniliform lumina, leaving entrapped minute air bubbles (seen in freshly mounted sections), suggesting the spongy cortex of the subgenera LETHARIELLA and CHLOREA. The algae occur as small colonies throughout the moderately lax medulla, not forming a separate layer between the cortex and medulla. The algal cells seem to be short, discrete cylinders, although packed in rounded colonies, suggesting that they may have come from filaments of *Trentepohlia* with nearly isodiametric cells, occasionally more filamentous as they push out along cracks in the cortex. The axis is solid and quite uniform with an occasional small bundle of brownish hyphae in the outer 50 μ.

Motyka mentions a plant from Anatolia, Ibidh dere, *H. Czeczott*, at Cracow, which has a solid axis and a K— medulla, tentatively referred to *U. syriaca*. Our plant may be a distinct species, but I dislike to describe a new taxon on a single incomplete plant.

ERITREA: without locality, *F. Gallina*, ex herb. Sbarbaro sub *U. plicata*, at Farlow Herb.

58. USNEA SUBLEPROSA Motyka, Lich. Gen. Usnea Stud. Monog. 605. 1938

Type: South Africa, Transvaal, Lydenburg, *Wilms*.

Thallus up to 20 cm. long, usually smaller (7 cm. in our plant), rigid, perhaps pendent, subglaucescent drying olive green (Motyka), (fuscous on larger branches shading to dark olive buff at the summits and ramuli in our plants); base penetrating crevices in the rock (broken off in our plants); lower portion about 1.5 cm. long, 1.5 mm. in diameter, black, forming an arc of about 90°, sympodially branched with very short internodes; principal axes flexuous, articulate, joints constricted at the ends, slightly inflated in the middle, up to 2 mm. in diameter below, of variable length, rarely annularly cracked, densely verrucose to subpapillate, the more slender lateral branches subarticulate, verrucae less dense and larger, forming slightly elevated soralia of isidiose soredia which appear farinose after the soredia are shed; ramuli subdistant, about 10 mm. long, curving toward the summits, verrucose and sorediose, slightly constricted at the base, annularly cracked, inflated in the lower portion, tapering to a short obtuse tip, often broken off; summits about 20 mm. long from dichotomy of the axis or lateral branch, about 0.5 mm. in diameter, resembling ramuli in structure.

Apothecia rare (absent in our plants), lateral to subterminal, up to 7 mm. in diameter; exciple uneven, sublacunose, verruculose and sorediose, sometimes ciliate; marginal cilia few or none, about as long as the diameter of the disc, rather thick,

obtuse, subarticulate, with farinose soredia; disc plane or somewhat deformed, flesh color, slightly or not pruinose.

KENYA: Guaso Nyiro, *G. M. Allen 1792 p. p.*, in Howe herb. sub *U. florida* v. *strigosa* Ach., at Farlow Herb.

CONGO: Mont Kahuz, about 3000 m., saxicole, *F. L. Hendrickx 1273.*

PORTUGESE MAIOMHE: Chiluango, *J. Gossweiler* (1919); rather young, papillae in dense longitudinal rows on some branches, not on others, giving an angular appearance.

59. USNEA LEDIENII (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 593. 1938. *Usnea strigosa* v. *Ledienii* Stein, Jahresber. Schles. Ges. Vaterl. Cultur 66:139. 1888.

Type: Cameroons, Buea near the caves, *Preuss.*

Thallus fruticose, erect, rigid, about 7 cm. tall, drying citrine drab, more slender branches and ramuli dark olive buff; base 3 mm. in diameter, a dense mass of root-like fibers penetrating the bark, slightly darker; densely sympodially branched at the base and rarely dichotomous above, branches up to 1.5 mm. in diameter below, tapering gradually upward, remaining rather thick to the summits, somewhat flexuous, slightly attenuate and articulate at the base, not or only very slightly articulate above, with simple annular cracks; terete, sparsely and irregularly tuberculate to subpapillate below, more closely so above, tubercles sometimes in rows but not close enough to form ridges, forming soralia of isidiose soredia, especially on the more slender branches and larger ramuli; ramuli quite close, some 1–3 mm. long, smooth, others up to 15 mm. long, tuberculate and sorediose, sometimes so densely so that they appear furfuraceous, axils right angles but the longer ramuli curve upward, flexuous.

Apothecia not abundant, subterminal on the main axes, up to 10 mm. in diameter, often deformed; exciple plane or deformed, smooth when young becoming uneven and foveolate or scrobiculate; marginal cilia not close, long and short intermixed, rarely longer than the diameter of the disc, relatively thick, the longer tuberculate and with secondary ramuli; disc nearly plane or deformed, chalky white pruinose; ascospores 7–10 μ in narrow asci.

The above description of apothecia is translated from Motyka, *loc. cit.*, as only a single young apothecium is present in our material.

CAMEROONS: forest above Buea, 1450 m., *F. W. H. Migeod 144 p. p. min.*

ANGOLA: Cuanza Sul, Amboim, Capir, near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991*; Benguella, country of the Ganguellas and Ambuellas, *J. Gossweiler*; both at Kew.

UGANDA: Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Elgon, 1290 m., on trees, *W. Small 218;* both at Kew.

60. USNEA HISPIDA Motyka, Lich. Gen. Usnea Stud. Monog. 589. 1938.

Type: Cameroons, "Huea" (*lapsus calami* for Buea?), corticole, *Lemperch.*

Thallus probably pendent, rather rigid, up to 15 cm. long, drying sepia to bone brown, the ramuli lighter, cinnamon buff; holdfast black, thin, very rugose, 5–6 mm. in diameter, nearly surrounding a small twig; base very short, rigid, sym-

podially branching into 8–10 branches which bend around the twig and hang down on both sides; about thrice dichotomous in the basal portion with internodes about 10 mm. long, rarely dichotomous near the summits; branches straight or slightly curved, with annular cracks in the basal internodes, then articulate in the middle portion of the principal axes, joints constricted at the ends, slightly inflated, 1.5–2 (–3) mm. in diameter, thinning at each dichotomy, the more slender branches annularly cracked but not distinctly articulate; surface with very dense long papillae with a few areas sparsely so; ramuli subdistant on the larger joints, rather close on the more slender branches, 2–10 mm. long (some longer and themselves ramulose may be young lateral branches), the shorter smooth, the longer low-tuberculate, tips acute to acuminate; summits short, slender with subterminal apothecial initials.

Apothecia abundant, mostly about 5 mm. in diameter, a few up to 10 (–15) mm., sessile about one third the way from the tip of stout ramuli or small lateral branches, cupuliform becoming plane or rarely revolute; exciple smooth or in very large apothecia with a few radial ridges and sparsely tuberculate; marginal cilia few, radiating, 3–4 mm. long, quite fragile, tips acute; disc concave to plane or somewhat convex, densely white-pruinose, becoming snuff brown in age.

In *Hendrickx 3679*, the apothecia are much larger than usual, the marginal cilia are closer and longer (up to 20 mm. long), exciple with occasional short ramuli or large spinules on some of the larger apothecia, not on others of equal size. There are suggestions that some of the papillae grow out to form small spinules which easily break off as propagula. The colors are lighter, perhaps because more recently collected.

CAMEROONS: Cameroon Mt., 390 m., *Collier 1169*, ex herb. Bot. Gard. Victoria; in Meyer Crater, 1930 m., on *Aquaria salicifolia*, *T. D. R. 917*, ex herb. Bot. Gard. Victoria; above Buea 1290 m., ramulicole, *F. W. H. Migeod 53*; all at Kew.

FERNANDO PO: [Santa Isabel Peak], 1610 m., *Gustavo Mann 682* (two plants, tangled with summits of *U. speciosa* and *Anaptychia leucomelaena*, glued to sheet, making it difficult to trace branching), at Kew.

SÃO THOMÉ: *Gustavo Mann*, at Kew.

CONGO: Route Kahusi, 2450 m., on *Hagenia*, *F. L. Hendrickx 3679*, in E. African Herb.

61. USNEA OCHROPHORA (Stzbgr.) Motyka, Lich. Gen. Usnea Stud. Monog. 254. 1936.

Usnea florida v. *ochrophora* Stzbgr. in herb.

Type: South Africa, Cape of Good Hope, Talbe Mt., *Peter MacOwan.*

Thallus erect, rather rigid, up to 10 cm. tall, ashy green, drying between Saccardo's umber and buffy brown on main axes, lateral branches and ramuli wood brown to avellaneous; holdfast a dark disc about 2.5 mm. in diameter, base 1 mm. in diameter below expanding to 1.5 mm. above, 2 mm. tall, branching sympodial with short internodes in the lower half; axils of lower branches 90°, upper acute;

main axis 1.5 mm. in diameter below, tapering to 0.5 mm. below the subterminal apothecium; subarticulate, joints very slightly inflated, annular cracks wide, exposing the medulla; lateral branches similar but only 0.8 mm. in diameter, slightly constricted at the base, quite closely and minutely papillate throughout, a few papillae growing out as short spinulose ramuli; ramuli subdistant, about 5 mm. long, tips acuminate, paler, bases slightly constricted and articulate, slightly inflated and minutely tuberculate, rarely with a secondary ramulus, rather fragile.

Apothecia 4–5 mm. in diameter, sessile to subterminal on the main axis and lateral branches, cupulate becoming plane; exciple smooth to slightly rugulose with a few papillae near the point of attachment; marginal cilia subdistant, radiating, 2–7 (–10) mm. long, sometimes forked near the base, similar to ramuli; disc concave to plane, chalky-pruinose.

SOUTH AFRICA: Cape of Good Hope, Hermansdorp District, Blue Lilies bush, *A. Woodcock.*

NYASALAND: Nyika plateau, 2340 m., ramicole, *L. J. Brass 17212,* in N. Y. Bot. Gard. (Vernay Nyasaland Exp.)

TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., ramulicole, in evergreen forest of steep slopes, *P. J. Greenway 6532.*

CONGO: Mt. Kahusi, ca. 2700 m., ramulicole, *F. L. Hendrickx 4300,* in E. African Herb.

KENYA: Mt. Kenya, 2250–2575 m., on bamboo twigs, *G. M. Allen* (only 4 cm. tall, cinnamon buff to pinkish buff, apothecia wholly lateral).

UGANDA: Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p. min.* (only 4.5 cm. tall with single lateral branch and immature apothecia).

ERITREA: without locality, *F. Gallina,* ex herb. Sbarbaro sub *U. plicata,* at Farlow.

62. USNEA SUBFOVEATA Dodge, Ann. Mo. Bot. Gard. 43: 395. 1956.

Type: Uganda, Bunyoro, Busingoro, on bark of *Jacaranda, I. R. Dale L69,* at Kew.

Thallus fruticose, erect, rigid, 5 cm. tall, between buffy olive and yellowish olive when dry; holdfast 3 mm. in diameter, not blackened, giving rise to three main axes, 1–1.5 mm. in diameter; closely dichotomous, branches slightly curved, axils 60–90°; articulate, joints about 10 mm. long, constricted at the ends, often bearing one or more lateral branches to a joint, more slender than the main axis, terete, subfoveolate from ridges of small papillae, many of which produce 1 or 2 spinulose isidia which break off, leaving a decorticate tip to the papilla; eramulose (small fragile lateral branches sometimes simulate ramuli).

Apothecia subterminal on the main axis and lateral branches, up to 9 mm. in diameter (often 2 develop less than 1 mm. apart so that the exciples are in contact but not concrescent), cupulate becoming plane, smooth to slightly impressed and verrucose or the larger ones few-ciliate; marginal cilia distant, up to 1.5 mm. long, annularly cracked and slightly constricted at the base, inflated in the middle and tapering to a subacute tip; disc concave to plane, smooth (deeply scrobiculate from folding of the thecium, teratological ?), ochraceous buff with a thin white pruina.

Cortex 30 μ thick, outer half brownish, closely fastigiate, inner half hyaline, hyphae more loosely interwoven, lumen about 2 μ; the whole in a gel; algal layer 15–20 μ thick, continuous, cells protococcoid, 6–8 μ in diameter; medulla 360 μ thick, the outer 35 μ densely woven, the rest almost wholly radial, of about 36 hyphae per circumference, dichotomous outward, very thick-walled, 5–6 μ in diameter, lumen 1 μ; axis 220 μ in diameter, solid, hyaline, of conglutinate, thick-walled hyphae.

This species is suggestive of *U. cristata,* which is more angled with a much larger hollow axis. *U. complanata* (FOVEATAE) has a thicker, complanate thallus without articulations or isidia and is partly ramulose. *Turrall 55 p. p. min.* is apparently a small moribund specimen, only about 2 cm. tall with apothecia 2 mm. in diameter.

SUDAN: without locality, *J. T. Bent,* at Kew.

KENYA: Northern Frontier Province, summit of Ajao hill, 1030 m., near Buna, on bushes, *I. R. Dale L71*; Mau Forest, Endabarrá, 2350 m., at edge of *Acacia* grove, on trees, *P. R. O. Bally B4947,* a small fragment; all at Kew.

UGANDA: Bunyoro, Busingoro, on bark of old *Jacaranda* tree, *I. R. Dale L69,* type, at Kew.

TANGANYIKA: Kilimanjaro, 2900–3045 m., on giant heather in clearings, *R. G. Turrall 55 p. p. min.,* at Kew.

63. USNEA TRACHYNA Motyka, Lich. Gen. Usnea Stud. Monog. 612. 1938.

Usnea barbata v. *aspera* Müll. Arg., Flora 73:336. 1890, *non alio loco.*

Type: Tanganyika, Pagani, *von Hoehnel,* at Turku.

Thallus in type specimen 7 cm. long (incomplete, in other specimens cited by Motyka shorter, fruticose, in our plants about 6 cm. tall), somewhat prostrate, subflaccid, ashy olive green (*fide* Motyka, in our plants warm sepia to Verona brown, ramuli wood brown); holdfast a disc 2 mm. in diameter, scarcely darkened, base 3 mm. tall, 1 mm. in diameter below, expanding to 2 mm. just under the first branch; branching sympodial or more often unilateral, the axis and first branch curving downward and apparently nearly prostrate, the other branches erect, axils nearly right angles; articulate, joints variable in length, ends constricted to 1 mm. in diameter or less, inflated to 1.2–1.5 mm. below, to 1 mm. just below the apothecia; terete, papillae subdistant below, rather close above, small, short-cylindric, or larger, subcapitate or somewhat coralloid (perhaps from regeneration after small ramuli have broken off as the tips are more or less decorticate); ramuli quite close, mostly broken off on the older joints, 1–10 mm. long, the shorter smooth, but annularly cracked, the longer tuberculate to small-papillate, the longest with secondary ramuli (probably young lateral branches).

Apothecia subterminal on lateral branches (often appearing terminal when the end of the branch has broken off), 5–8 mm. in diameter, nearly plane, but margin somewhat inrolled and folded in drying; exciple smooth, subfoveolate and partly minutely papillate on the larger ones; marginal cilia subdistant, 3–4 mm. long,

similar to ramuli but very fragile and mostly broken off, leaving only a few short young cilia; disc plane, pale olive buff pruinose.

Ellis 4 is rather short, 3–4 cm. tall, with a thinner cortex (40–55 μ) but agrees otherwise. *Dale L40* is 4 cm. tall, more erect and densely ramulose, although it is abundantly fertile with apothecia up to 7 mm. in diameter.

ERITREA: Filfa Pass, *P. E. Ellis 4*, at Kew.
KENYA: Chyulu Hills, *H. D. van Someren*, in E. African Herb.
UGANDA: Toro, Fort Portal, 1630 m., *I. R. Dale L40*; Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p.*; both at Kew.
TANGANYIKA: Kilimanjaro, Marangu-Bismarck, 2100 m., *R. G. Turrall 37*, at Kew; Maruessa, *Hildebrandt*, ex Herb. Sbarbaro, at Farlow Herb.

64. USNEA SCUTATA Motyka, Lich. Gen. Usnea Stud. Monog. 602. 1938.

Type: Cameroun Française, Ntem, 950 m., *Ledermann*.

Thallus fruticose, rigid, dirty glaucescent olive green (light brownish olive shading to Isabella color on slender branches and ramuli in our plants), attached by rooting fibers which penetrate the outer layer of the bark, without a visible holdfast, base about 3 mm. tall, 1 mm. in diameter below, expanding to 2 mm. at the first branch, rarely unbranched below, tapering gradually to 1 mm. in diameter below the apothecium; once or twice dichotomous above the base with very short internodes, then unequally dichotomous above, axils about 90°; articulate, the joints inflated, ends constricted, rather long, bearing 3–4 lateral branches 1 mm. or less in diameter, usually terminated by apothecia, a few sterile ones ending in a tuft of 3–4 slender branches about the size of the larger ramuli but minutely ramulose; terete, verruculose-papillate, very few papillae on the lower joints, denser above on low reticulate ridges and the surface appearing subfoveolate, some of the more cylindric papillae growing out as minute ramuli, leaving scars as they break off, but not sorediose; ramuli irregularly disposed, rather dense on some branches, distant on others, 2–3 mm. long, tips obtuse, annularly cracked and subinflated, smooth, some probably developing as small lateral branches, minutely papillate and minutely ramulose.

Apothecia subterminal, cupulate becoming plane, up to 15 mm. in diameter; exciple densely verruculose-papillate; marginal cilia in two ranks, distant, 2–3 mm. long, resembling ramuli; disc flesh color, covered by a dense white pruina.

Our material agrees well with Motyka's description except the apothecia are only 3–5 mm. in diameter and the disc is concave. *Deighton 3503* has more dense ramuli and the papillae in less distinct rows. *Allen 1779* from Kenya is larger in all dimensions but otherwise agrees. Thallus 10 cm. tall, rather flaccid; apothecia up to 23 mm. in diameter; cortex 130 μ thick, highly gelified, outer 20 μ deep brownish, of very loosely woven, predominantly radial hyphae, denser just below the colored zone; algal layer about 70 μ thick, of colonies of *Trebouxia*, forming a nearly continuous layer; medulla 670 μ thick, of very loosely woven thick-walled hyphae 6–7 μ in diameter, predominantly radial and somewhat more densely woven in a narrow zone just below the algal layer; axis 410 μ in diameter, solid, of longi-

tudinal, relatively thick-walled hyphae, lumen about 3 μ, becoming brownish in age. The large size is suggestive of *U. ruvidescens*, but the proportions of cortex, medulla and axis are nearer those of *U. scutata*, as are the conspicuous papillae.

SIERRA LEONE: Lei, Sankon Biriwa, 1930 m., *F. C. Deighton 3503*, at Kew.

ANGOLA: Northeast Lunda, Dundo, 750 m., near the Luachima River, on tall trees of the gallery wood, *J. Gossweiler 13928*, at Kew.

KENYA: Lake Ngunga, 1770 m., on branches of trees, *G. M. Allen 1779*, in Howe herb. at Farlow Herb.

65. USNEA ALBOMACULATA Motyka, Lich. Gen. Usnea Stud. Monog. 620. 1938.

Type: Ethiopia, Isaac Debr., Semenbachgebirge, *Stender*.

Thallus pendent, 7–9 cm. long, probably olive buff or lighter when living, larger branches between wood brown and dark olive buff, slender branches and ramuli olive buff or pale olive buff after 3 years in the herbarium (pale fuscous after 75 years); holdfast conic, about 2.5 mm. in diameter, of radiating, concrescent blackened root-like fibers, base 1 mm. in diameter below expanding to 1.5 mm. above, about 3 mm. long; branching unequally dichotomous below, closer and more sympodial above; articulate and 1.5 (–2.5) mm. in diameter below, tapering to about 1 mm. and scarcely articulate below the apothecia, with minute indistinct verrucae and large pseudocyphelliform elevated white ecorticate tubercles (apparently from regeneration where a small branch has broken off from unusually great proliferation of the medulla, not truly farinose-sorediose), round or somewhat oblong, more closely verrucose to minutely tuberculate above and subfoveate just under the apothecia; ramuli dense on the smaller branches, 2–8 mm. long, ascending (the longer perhaps young branches as they are verruculose at the base and sometimes branched above), articulate and constricted at the base, inflated, tapering to an acute tip.

Apothecia sessile on the smaller branches as well as terminal, 4–6 (–15) mm. in diameter, concave; exciple smooth or subpapillate near the base with a few small ramuli; marginal cilia close, thick, conic, slightly constricted at the base with acute tips, in two rows, the outer longer, sometimes branched, the inner shorter, simple; disc concave, flesh color, slightly white pruinose.

Chipp 57 p. p. is tentatively referred here although the surface is almost papillate, the ramuli are less dense, and the white pseudocyphelliform tubercles are smaller and rarer.

ETHIOPIA: Simien, Mindigabsa, ramulicole, *H. Scott 323*, at Kew.

SUDAN: Onyiro, Issore, 1770 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57 p. p.*; Mt. Kinnelli, on pole and cairn, 3360 m., *T. F. Chipp 64*, juvenile, tangled with *U. maculata* Stirton, both at Kew.

66. USNEA BORNMUELLERI Steiner, Verhandl. Zool. Bot. Ges. Wien 53:227. 1903.

Type: Cameroons, Cameroon Mt., *Alfred Bornmueller*, portion of cotype in Howe herb. com. Zahlbruckner, at Farlow Herb.

Thallus suberect to prostrate, 5–8 cm. tall, somewhat flaccid, "gelblich-graugrun" (Milbraed) when fresh, drying olive green (Motyka) but brownish olive below shading to Isabella color in our plants; holdfast subhemispheric, 3 mm. or more in diameter, black, the root-like fibers broken in collecting; main axis 1 mm. in diameter, rapidly expanding to 2 mm., closely dichotomous near the base, then less frequently so in the upper portion and again very closely so at the summits, axils nearly 90° angles; branches somewhat curved, articulate, joints inflated up to 2.5 mm. in diameter in lower portion, tapering to 0.5 mm. just below the tips, 5–12 mm. long, terete, cracked between the joints but not separated (unless roughly handled in collecting); surface irregularly verrucose, sometimes in short ecorticate ridges on the lower joints, with somewhat larger, low tubercles on the upper joints, producing isidiose soredia which soon break off, leaving white punctiform scars, the larger ones resembling small farinose soredia; summits densely branched, somewhat deformed by small tubercles, not soraliate, tips blackened (much less so than in species of the subgenus *Neuropogon*).

Cortex 60 μ thick, brownish, gelified, very hard, fastigiate, lumen of hyphae about 1 μ; algae in scattered discrete colonies, about 35 μ in diameter, cells protococcoid, 6–7 μ in diameter; medulla about 980 μ thick, of very loosely woven hyphae 6–7 μ in diameter, lumen 1 μ, periclinal next the algal colonies and cortex, radial within; axis 200 μ in diameter, outer surface slightly irregular, of thick-walled longitudinal, conglutinate hyphae.

CAMEROONS: Cameroon Mt., grasslands, *Alfred Bornmueller*, portion of type, com. Zahlbruckner in Howe herb. at Farlow Herb.; mountain above Buea, 3900 m., saxicole, in grasslands above tree line, *J. Milbraed 10913*, at Kew; 1500 m., *F. W. H. Migeod 144*, at Kew; 400 m., *Pollier 1169bis*, at Kew.

67. USNEA FLOTOWII Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.
Usnea barbata v. *cornuta* Flotow, Linnaea 17:16. 1843, *p. p.*

Type: Ethiopia, Mont. Simens., 3000–4000 m., saxicole, *Schimper.*

Thallus caespitose-fruticose, suberect, about 10 cm. tall, rigid; base hemispheric, 5 mm. in diameter, sympodially branched about 2 mm. above, forming prostrate principal axes from which arise erect lateral branches on the upper side, very close in the proximal half of some axes, less so in others; lateral branches dichotomous, some once, others several times, especially in the upper portion, making a very intricate mass; main axes and secondary branches 2 mm. in diameter, tapering at each dichotomy to short, slender summits; articulate on main axes and secondary branches in lower portions, joints constricted at the ends, somewhat inflated, simply cracked above, surface closely and minutely white-tuberculate except the basal joints, the tubercles often in rows, forming reticulations or, where longitudinal, appearing slightly angular, mostly forming soralia of isidiose soredia; most axes and secondary branches eramulose, a few densely to sparsely ramulose; shorter ramuli 1–2 mm. long, nearly smooth, the larger 10–15 mm. long, coarser,

more fragile, a few branched, closely tuberculate to subpapillate, producing soredia; summits short, obtuse, rugose, farinose from soredia.

Jarrett 402 is a single moribund fragment closely related to this species but may be new. It is in too poor condition to describe; it is arboricole and comes from a much lower altitude.

ETHIOPIA: Simien, Mindigabsa, *H. Scott 323 c*, moribund fragments, portions in Howe herb. com. Zahlbruckner, at Farlow Herb.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

UGANDA: Kigezi, Muhavura, 4230 m., saxicole, among mosses, *A. S. Thomas 1114*; Ruizi River, 1390 m., arboricole, *T. Jarrett 402*; both at Kew.

68. USNEA SERPENTARIA Motyka, Webbia 8:392. 1952.

Usnea Flotowii subsp. *serpentaria* Motyka, Lich. Gen. Usnea Stud. Monog. 625. 1938.

Type: Ethiopia, Mont. Simens. near Dibell, saxicole, 3000–4000 m., *Schimper.*

Thallus erect, forming dense tufts, 9 cm. tall from a common holdfast, up to 9 mm. in diameter with dense dichotomously branched root-like fibers about 2 mm. long; branches simple or dichotomous just above the base, often again dichotomous about 1 cm. above the base and again about 3 cm., then more frequently dichotomous, the ultimate branches sparingly ramulose; base blackened to the first dichotomy, shading upward from Saccardo's umber through buffy citrine to old gold at the summits and ramuli; branches 2 mm. in diameter below, slightly flexuous, thinner at each dichotomy, ultimate branches and ramuli 0.2–0.3 mm. in diameter at the base, tapering upward to obtuse, dark brown tips, not articulate nor inflated, subfoveate with low flat ridges, cortex subareolate but not flaking off on the larger branches, the smaller branches less rugose and sparsely papillate, the papillae short and broad, forming minute pseudocyphellae on all but the slender ramuli; ramuli rare or absent on some branches, unilateral on others, varying from 2 to 20 mm. long, curved upward. Only one moribund subterminal apothecium present in our plants.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

69. USNEA CAPENSIS Motyka, Lich. Gen. Usnea Stud. Monog. 321. 1937.

Type: S. Africa, Orange Free State, Taaboschkranz, *Rehman.*

Thallus caespitose-fruticose, erect, about 5 cm. tall, pale ashy olive green (buffy olive in our plants); holdfast a black cone, 4 mm. in diameter, 2 mm. high, adherent to the rock, giving rise to about two axes 1.5 mm. in diameter, expanding to 2 mm. at the lowest dichotomy, rather closely but unequally dichotomous throughout; articulate, joints constricted at the ends, subinflated below, relatively long, tapering upward but relatively thick to the summits, subareolate below, smooth above (very faintly verrucose under 12× magnification); ramuli very dense but very fragile, up to 5 mm. long, tips acute, often blackened but more

often broken off and then digitiform, slightly constricted at the base, subinflated, densely beset with minute spinules with blackened tips near the summits; summits finally curved, 0.2–0.3 mm. in diameter, grossly tuberculate with isidiose soredia, appearing farinose after the soredia are shed. Apothecia not seen.

Thomas 3631 is smaller, about 4 cm. tall, and very few of the sorediose recurved summits have been formed, evidently the decadent spinules serving as isidia. The *Forbes* specimen from Nyasaland is 5 cm. tall and more sparingly branched; it may be a juvenile form of *U. transvaalensis,* although it agrees in other vegetative characters with *U. capensis.*

UGANDA: Karamoja, Napak, 2250 m., on rocks in mountain grassland, *A. S. Thomas 3631,* in E. African Herb.

NYASALAND: Mt. Mlangi, 1930–2250 m., *A. P. S. Forbes* (6 July 1939), in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, without locality, *Mund & Maire,* in Tuckerman herb. sub *U. barbata* v. *hirta,* at Farlow Herb.

70. USNEA PULVINATA Fries in Lehmann, Pl. Preiss. 2:145. 1846-47.

Type: Western Australia, *Preiss.*

Thallus up to 3.5 cm. tall, erect, fruticose, very rigid, pale greenish, drying olive ochre to honey yellow in the herbarium; holdfast of coarse radiating rootlets penetrating between the rock crystals, somewhat blackened and verrucose; branching into three or more primary axes about 1 mm. in diameter, lowest internode variable in length, up to 8 mm., then twice or thrice closely dichotomous and rarely so above, angles about 45° and the branches curving upward, terete, surface smooth except for scars of broken ramuli; ramuli variable in length, 1–10 mm. long, slightly constricted at the base and inflated in the middle, about 0.2 mm. in diameter, curving upward and tapering to obtuse tips, some growing out as slender lateral branches and again short-ramulose, surface tuberculate, forming small soralia of isidiose soredia, usually black-tipped and appearing farinose after the isidia are shed, in old plants the soralia more or less confluent, giving a furfuraceous appearance under 12× magnification.

Apothecia absent in our material, reported by Motyka as terminal, about 3 mm. in diameter; exciple smooth, sometimes with tubercles; marginal cilia short, dense, thick and obtuse; disc somewhat concave, yellowish flesh color, slightly pruinose.

Cortex about 110 μ thick, fastigiate and brownish in the outer 30 μ, loosely and irregularly woven below, imbedded in a hyaline gel; algal layer of discrete colonies of *Trebouxia,* about 30 μ in diameter, forming a nearly continuous layer, cells 4–7 μ in diameter, somewhat polyhedral from mutual pressure; medulla 75–80 μ thick, white, K—, densely woven, of predominantly periclinal hyphae 6–7 μ in diameter, lumen 1 μ, inner 10–15 μ brown next the axis; axis 700 μ in diameter, outer 200 μ of interlaced transverse hyphae, predominantly periclinal, the central cylinder predominantly of longitudinal hyphae with more slender lumina and much more transparent so that under lower magnifications the axis appears hollow.

The Robillard plant is somewhat doubtfully referred here, as the cortex and axis are thinner and the soredia are less developed. The axis is uniformly composed of longitudinal hyphae.

MADAGASCAR: Imerina, Andrangoloaka, saxicole, *Hildebrandt 2172* (3 collections), at Farlow Herb., Province of Betafo, *native collector,* spring 1901, ex herb. E. G. Paris, 1904 (2 specimens), at Farlow Herb.

MAURITIUS: without locality, *Robillard* ex Gray Herb. sub *U. florida* v. *strigosa* Ach., at Farlow Herb.

71. USNEA MYRIOCLADA (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 6:588. 1930.
Usnea barbata v. *myrioclada* Müll. Arg., Bot. Jahrb. [Engler] 20:244. 1894.

Type: Tanganyika, Usambara, Derema, *Fischer.*

Thallus erect, subfruticose, about 5 cm. tall, pale glaucescent green (Motyka, axes between buffy brown and citrine drab, ramuli between dark olive buff and deep olive buff in our plants); base of coarse rooting fibres penetrating dead wood; closely sympodially branched at the base and frequently so throughout, axils nearly right angles, becoming nearly dichotomous below the summits; main axes subarticulate, joints very slightly inflated, rather long, very densely ramulose below, appearing smooth between the ramuli but slightly verruculose under 36× magnification; ramuli mostly 1–2 (–5) mm. long, slightly constricted at the base, annularly cracked, slightly inflated, fragile, many broken off at the base, giving a coarsely verrucose appearance, abruptly tapering to an acute black tip; slender branches and summits nearly devoid of ramuli, closely tuberculate, producing soralia of isidiose soredia which may appear farinose after the soredia are shed; summits of the main axes all broken off, those of slender branches densely coralloid, branched.

A fragment of another plant in the collection is fertile; the vegetative portion is identical with that of the sterile plant. Apothecia sessile on slender branches, 3 mm. in diameter, cupulate; exciple densely ramulose with short conical ramuli, appearing subfoveolate between them; marginal cilia erect, very dense, in two rows, less than 1 mm. long, resembling small ramuli; disc concave, flesh color, densely white-pruinose.

In *Gossweiler 9991*, the summits are nearly intact, tapering to acute tips, not coralloid.

ANGOLA: Cuanza Sul, Amboin near Carloaongo-Cuvo River, 1000 m., on dead trees, *J. Gossweiler 9991*, at Kew.

SOUTHERN RHODESIA: Mazoe District, 1320 m., on dead wood, *Frederick Eyles 419*, at Kew.

72. USNEA LYNGEI Motyka, Lich. Gen. Usnea Stud. Monog. 411. 1937.

Type: St. Helena, near tomb of Napoleon, collector unknown, at Oslo.

Thallus pendent, rather flaccid, about 20 cm. long, pale ashy (main axes olive brown below, upper portions and ramuli deep olive buff in our plants); base about

10 mm. long, 0.9 mm. in diameter, lower part black, closely and regularly annularly cracked; closely dichotomous at nearly right angles just above the base, then dichotomous at acute angles with relatively short internodes throughout, minutely tuberculate throughout, each white tubercle bearing a few isidia; ramuli somewhat irregularly disposed, variable in length up to 30 mm. long, flexuous, slender, annularly cracked, not tuberculate or very minutely so at the base of the longer ramuli, tips acuminate but mostly broken off.

A single apothecial initial seen, lateral at the base of a large ramulus, but heavily infected by a parasite before the initial reached 1 mm. in diameter. *Warnecke 107* is too fragmentary for certain determination.

TOGO: *Warnecke 107,* in E. African Herb.
FERNANDO PO: [Santa Isabel Peak], 2900 m., *Gustavo Mann 682 p. p. min.,* at Kew.
ST. HELENA: without locality, *J. D. Hooker,* in Taylor herb. at Farlow Herb.

73. USNEA GOSSWEILERI Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Angola, Cuanza Sul, Amboim, Capir near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991,* at Kew.

Thallus erect, fruticose, 5–6 cm. tall, between deep olive buff and tea green; holdfast about 4 mm. in diameter, 2 mm. thick; polychotomous at the top of the holdfast into 7–8 branches about 1.5 mm. in diameter, again densely branched 7–10 mm. above, then rarely branched sympodially in the mid-portion, branches about 1 mm. in diameter, dichotomously branched above, thinning at each dichotomy, annularly cracked but not inflated; surface closely verrucose-tuberculate, forming isidiose soredia, appearing spinulose where the tubercles are crowded and finally farinose after the isidia are shed; ramuli 2–3 (–5) mm. long, irregularly dense, the shorter smooth, the longer minutely tuberculate with acute, often blackened tips; sterile summits short, relatively thick, but tips acute.

Apothecia rare, sessile on the main axes some distance below the summits, or subterminal, 3 mm. in diameter (perhaps immature); exciple smooth; marginal cilia subdistant, annularly cracked at the base, 1–2 mm. long, conic, the longer sometimes dichotomous and minutely tuberculate; disc carneous, white-pruinose.

Cortex 85–100 μ thick, fastigiate, highly gelified, hyphal lumina subdistant within, repeatedly dichotomous in the outer 30 μ where the gel is more deeply stained but without crystals; algal layer 40–60 μ thick, of discrete colonies of *Trebouxia,* about 25 μ in diameter, cells 5–6 μ in diameter, sometimes scattered, sometimes aggregated into a nearly continuous layer; medulla about 160 μ thick, of thick-walled hyphae about 3 μ in diameter, very densely interwoven and heavily nubilated with hyaline or slightly brownish crystals, very lax in the inner 25 μ; axis 230 μ in diameter, of thick-walled longitudinal hyphae, conglutinate in the outer portion, less compact toward the center, with longitudinal air spaces up to 10 μ in diameter between the strands of hyphae.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo River, 1000 m., on dead trees, *J. Gossweiler 9991,* at Kew.

74. Usnea torrida Motyka, Lich. Gen. Usnea Stud. Monog. 327. 1937.

Type: Congo, without locality or collector, in British Museum.

Thallus about 5 cm. tall, erect, rather rigid, citrine drab; holdfast penetrating cracks of bark on twigs; base up to 5 mm. long, about 1 mm. in diameter, scarcely blackened; branching once to thrice dichotomous at the base, occasionally so above; branches variously curved upward, slightly constricted at the base, soon about 1 mm. in diameter, tapering upward; surface smooth between the very dense ramuli; ramuli 0.5–2 mm. long, tips acute, straight or slightly curved upward, occasionally growing out to 5 mm. long as small lateral branches, again sparingly ramulose; on the lower portion the ramuli break off so that the lower internodes appear tuberculate to papillate.

Apothecia terminal, up to 3 mm. in diameter, cupulate becoming nearly plane; exciple closely small-ramulose (not as densely as on the branches); marginal cilia dense, 3–4 mm. long, annularly cracked and bearing a few ramuli; disc concave, flesh color, densely white-pruinose.

The Nyasaland plant is a fragment, less densely ramulose but it agrees otherwise.

KENYA: Northern Frontier Province, summit of Ajao hill, 1030 m., near Buna, on bushes, *I. R. Dale L71 p. p.*, at Kew.

ANGOLA: Northeastern Lunda, Chitato, Dundo near Rio Luachima, 750 m. (Expl. Companhia de Diamantes de Angola), on tall trees, *J. Gossweiler 13928*; Benguella, country of the Ganguellas and Ambuellas, *J. Gossweiler*; both at Kew.

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16846* (Vernay Nyasaland Exp. 1946), in N. Y. Bot. Gard. Herb., a fragment tangled with *U. Vainioana* Zahlbr.

75. Usnea picta (Steiner) Motyka, Lich. Gen. Usnea Stud. Monog. 325. 1937.

Usnea ceratina v. *picta* Steiner, Sitzungsber. K. Akad. Wiss. Wien, math.-naturw. Cl. 106:1:210. 1897.

Type: Kenya, Machakos, corticole, *Liechtenstein.*

Thallus fruticose, rigid, ashy green, 8–10 cm. tall, base very rigid, several times subsympodially branched above the base, axils nearly right angles; branches irregularly divergent, up to 2 mm. in diameter throughout most of the length, tapering gradually to short, branched summits, nearly straight, slightly constricted at the bases, with verruciform papillae, obtuse, denser in the upper portion of the branches; ramuli rather thick, rigid, aculeiform, perpendicular to the branches, tips acute, often branched.

Apothecia abundant, terminal, up to 20 mm. in diameter, nearly plane and densely pruinose when young, becoming convex, often plicate-rugose in the center when old; exciple smooth, glabrous; marginal cilia rather rare, 5–10 mm. long, rigid, conical; disc the same color as the thallus, slightly pruinose; epithecium yellowish; ascospores $6 \times 10\ \mu$.

Cortex about 100 μ thick, very hard, chondroid, dilacerate within and perforate in places; medulla about 200 μ thick, dense, K— or yellow next the axis; axis 420 μ in diameter, somewhat effigurate.

I have not seen material certainly referable here. The material Motyka referred to *U. picta* is evidently variable, as three of the six specimens cited are annotated as not typical. *U. isabellina* Dodge from the Northern Frontier Province of Kenya is related to *U. picta*; perhaps the same as the specimen cited by Motyka from southern Usambara, *H. Meyer*, "forma thallo substramineo, haud exacte certa." The Nyasaland plant is closer to Motyka's description but the axes are up to 3.2 mm. in diameter, apothecia only 5 mm. in diameter and the axis 2650 μ in diameter, quite lacerate but not distinctly hollow. I hesitate to describe another new taxon in this group until I have seen more material.

NYASALAND: Zomba Plateau, 1820 m., saxicole, *L. J. Brass 16166* (Vernay Nyasaland Exp.), in N. Y. Bot. Gard. Herb.

76. USNEA ISABELLINA Dodge, Ann. Mo. Bot. Gard. 43:395. 1956.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L71*, at Kew.

Thallus erect, fruticose, rigid, 7 cm. tall, Isabella color below, shading to chamois above; holdfast 8 mm. in diameter, giving rise to about 10 main axes 1–1.8 mm. in diameter, some branching almost at the base, some up to 20 mm. to the first branch, infrequently dichotomous to subsympodially branched above, terete; cortex smooth, closely annularly cracked and subareolate below, less so above, appearing coarsely papillate from the ramuli breaking off about 0.2 mm. from their bases; ramuli dense, quite fragile, 2–4 mm. long, coarse, slightly verrucose but not becoming sorediate, tips often slightly blackened, some longer ramuli growing out as small lateral branches; ultimate branches up to 40 mm. long, tapering slowly, tips broken off.

Apothecia rather rare, about 5 mm. in diameter, sessile some distance below the tips of the branches, plane to subrevolute; exciple smooth to slightly rugose; marginal cilia fragile, of variable length up to more than 3 mm. long, resembling ramuli; disc avellaneous, slightly white-pruinose.

Cortex 40–50 μ thick, fastigiate, forming a relatively thin-walled pseudoparenchyma, cells 5–6 μ in diameter, the outer 25 μ heavily nubilated with minute brownish crystals; algae *Trebouxia*, in small discrete colonies, some up to 40 μ in diameter, cells 6–8 μ in diameter; medulla 65–80–120 μ thick, of slender (3 μ in diameter) hyphae very densely interwoven and heavily nubilated with minute brownish crystals; axis 500 μ thick, of predominantly longitudinal, thick-walled hyphae about 3 μ in diameter, lumen 1–1.5 μ.

This species seems closest to *U. picta* (Steiner) Motyka, and perhaps the specimen cited by Motyka from Tanganyika, southern Usambara, *H. Meyer* "forma thallo substramineo, haud exacte certa" may belong here. *U. isabellina* differs from

U. picta in color, size, of parts, thinner cortex and medulla and much thicker axis.

KENYA: Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L71*, at Kew.

77. USNEA HORRIDULA (Müll. Arg.) Motyka, Lich. Gen. Usnea Stud. Monog. 335. 1937.

Usnea longissima v. *horridula* Müll. Arg., Flora 74:372. 1891.

Type: South Africa, Moorn River near Port Natal (Durban), *Plant.*

Thallus pendent to creeping, up to 30 cm. long, shorter in our plants, olive green drying Mars brown to russet on the main branches, ramuli and tips of branches cinnamon buff, reddish-maculate; base conic, about 2 mm. in diameter, composed of black rooting fibers penetrating the bark, 7 mm. tall, 1.5 mm. in diameter, branching dichotomous at nearly right angles, then curving downwards and flexuous but not parallel, tapering gradually to the short capillaceous summits; cortex cracked and areolate below, verrucose, becoming papillate above the second axil, many papillae growing out to form very dense ramuli about 2 mm. long, annularly cracked at the base, minutely tuberculate, forming soredia, others smoother, up to 7–8 mm. long (perhaps young branches), rather fragile, leaving slightly elevated farinose scars; summits about 10 mm. long, densely dichotomous, slender, tapering to acute tips.

Cortex very variable in thickness in the same section, 80–135 μ, the outer 55 μ of predominantly periclinal branched hyphae, rather closely packed, reddish, the rest more loosely woven, all imbedded in a yellowish gel, paler next the algal layer; algal layer of discrete colonies about 35 μ in diameter, cells *Trebouxia*, about 8 μ in diameter, in some places the colonies quite close, in others distant and dying off; medulla about 210 μ thick, the outer 70 μ pale, of predominantly periclinal hyphae, the rest of very densely woven, very thick-walled hyphae 3 μ in diameter, obscured by brownish crystals; axis 600 μ in diameter, very dense and hyaline with scattered brownish areas about 35 μ in diameter, due to minute brownish crystals which obscure the structure.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

78. USNEA DALEI Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Kenya, Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L70*, at Kew.

Thallus pendent, subrigid, more than 16 cm. long, probably up to 40 cm.; main axes drying deep olive buff, rarely pink-maculate in younger plants and in the more slender distal portions of older plants, the lower portions of the axes of older plants becoming orange cinnamon, the ramuli remaining deep olive buff; holdfast of rootlike fibers penetrating the bark, base about 1 mm. in diameter and 2 mm. tall, terete, somewhat blackened and annulate; closely dichotomous to sympodially

branched just above the base, then rarely dichotomous with long internodes throughout; main axes about 1 mm. in diameter, tapering gradually to the tips, acutely few-angled from concrescent rows of papilliform tubercles and the complanate bases of the ramuli, sulcate between the ridges, with a few scattered papilliform tubercles in the furrows; the tubercles growing out as coarse spinules serving as isidia; quite closely ramulose throughout along the acute corticate ridges, mostly about 4 mm. long, nearly cylindric, smooth with rather obtuse tips, a few up to 15 mm. long, curved or flexuous, closely tuberculate with relatively large tubercles in the lower portion, each bearing a few spinules; summits broken off, but such fragments as are present suggest that they are slender, unbranched and not capillaceous.

Cortex 50–55 μ thick, fastigiate, of thick-walled gelified hyphae, the outer 20 μ very deeply staining; algal layer 40 μ thick, a continuous layer of protococcoid cells 8 μ in diameter; medulla 250 μ thick, of thick-walled hyphae 3 μ in diameter, very densely woven next the algal layer and the axis, very loosely woven between; axis 550 μ in diameter, nearly circular in cross-section, the outer 40–50 μ of longitudinal, conglutinate thick-walled hyphae, the rest with single coarse brown hyphae 8 μ in diameter scattered throughout the sclerenchyma, giving the appearance of a section of a monocotyledonous stem such as that of maize.

U. Dalei suggests *U. decipiens* v. *Rhodesiana* Dodge, which is more angled with farinose soredia and which lacks any suggestion of a reddish color on the older axes. *U. Dalei* is the only sulcate species of the SETULOSAE, RUBIGINEAE, somewhat parallel to *U. chloreoides* (GONIODES), but is quite distinct in color and other characters. None of the species of the sulcate subsections, GONIODES nor SULCATAE, bear tubercles in the furrows, nor develop a reddish color.

KENYA: Northern Frontier Province, near Buna, summit of Ajao hill, 1030 m., on bushes, *I. R. Dale L70*, at Kew.

79. USNEA ERUBESCENS (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 333. 1937.

Usnea articulata f. *erubescens* Stein in H. Meyer, Ostafrikanische Gletscherfahrten, p. 314. 1890; [tr. E. H. S. Calder] Across East African Glaciers, 353. 1891 (with very brief description); Müll. Arg., Flora 73:336. 1890, *nom. nud.*

Usnea barbata v. *articulata* f. *erubescens* Stein, Jahresber. Schles. Ges. Vaterl. Kultur 66:134. 1888, *nom. nud.*

Type: Tanganyika, Kilimanjaro, at tree-line, 3000 m., *H. Meyer*, in Mus. Bot. Univ. Breslau.

Thallus pendent or possibly prostrate, about 20 cm. long, flaccid, drying reddish fuscidulous, dull; base not seen, sparingly dichotomously branched, one branch usually better-developed than the other; branches irregularly curved, up to 2 mm. in diameter; articulate, joints about 1 cm. long, inflated, constricted at the ends,

alternating with short cylindrical joints 0.3 mm. long, some of the larger joints deformed, rugulose and foveolate, almost epapillate, with minute tubercles along the ridges, other large joints smooth; ramuli absent; summits closely branched. Apothecia and soredia not seen.

Cortex about 30 μ thick, soft, fuscidulous; medulla up to 400 μ thick, very lax, white, K—, of irregularly woven hyphae; axis 120–150 μ in diameter, irregular in cross section.

Besides the specimen upon which Motyka based his description, Hans Meyer collected another among mosses of the grasslands at 4000 m., "mit gelbrothen Lager . . . " evidently smaller as he refers to the specimen from 3000 m. as "in sehr kräftigen langbärtigen Exemplaren." *Thomas 619* from Mt. Elgon, 4420 m., may be this entity. It is 5–8 cm. long, ochraceous tawny to ochraceous buff, alternation of long and short joints present but somewhat irregularly so, summits (upper centimeter) rather abruptly more slender, not articulate, slightly tuberculate but not sorediose and chamois to colonial buff. Only more material can show whether our plants are ecologic variants from higher altitudes or whether they represent a distinct taxon. Our plants somewhat resemble the more rigid *U. terricola* Dodge from Cameroons, which shows conspicuous soredia when much younger and comes from a lower altitude. If our reference of the Uganda material is correct and from Motyka's description, *U. erubescens* Motyka is much more closely related to the ARTICULATAE or the AMOENAE, in spite of its reddish color, than to the SETULOSAE, RUBIGINEAE, where Motyka places it.

UGANDA: Mt. Elgon, Masaba, 4420 m., on rocks in alpine meadow, *A. S. Thomas 619*, at Kew.

80. USNEA SUBFLORIDA (Zahlbr.) Motyka, Lich. Gen. Usnea Stud. Monog. 335. 1937.

Usnea Steineri v. *subflorida* Zahlbr., Bot. Jahrb. [Engler] 60:541. 1926.

Type: Tanganyika, Meru District, *Fassmann.*

Thallus erect, rigid, fruticose, 4–5 cm. tall, roods brown to pecan brown to wood brown and avellaneous in South African specimens (under 12× magnification irregularly light yellowish olive with coral red spots, reddish fuscous spotted with greenish fuscous, *fide* Motyka); holdfast 3 mm. in diameter, hemispheric, of coarse, branched rootlets, nearly black, base about 1 mm. in diameter below expanding to 1.5 mm. at the first dichotomy, about 5 mm. tall; thrice dichotomous with short internodes just above the base, axes about once dichotomous above; branches straight or curved, about 1.5 mm. in diameter below, tapering to 1 mm. below the apothecia; articulate, joints long, inflated below and tapering above, constricted at the ends, terete, papillose, some papillae forming spinules which break off as isidia; ramuli rather dense, 3–5 mm. long, the longer slightly tuberculate, tips acuminate but mostly breaking off, leaving an obtuse end as the cortex regenerates.

Apothecia up to 6 mm. in diameter, subterminal but appearing terminal when they mature, the branch often passing within the exciple and the tip emerging as a stouter cilium, cupulate to nearly plane; exciple with branched radial ridges becoming subfoveate, slightly tuberculate along the ridges; marginal cilia moderately close to subdistant, up to 4 mm. long, radiating, straight or flexuous, annularly cracked at the base, tapering to acute tips, maculate, the larger tuberculate; disc densely white pruinose when young, becoming dark flesh color in age.

KENYA: Mau forest, Endabarra, 2355 m., on trees at edge of *Acacia* grove forest, *P. R. O. Bally B4947 p. p. min.*, at Kew.

CONGO: Mt. Kahusi, 2700 m., ramulicole, *F. L. Hendrickx 4300*, small and moribund, in E. African Herb.

SOUTH AFRICA: Transvaal, Zoutpansberg district, near "Punch Bowl" Inn, on decaying tree trunks, *O. Almborn*, Lich. Afric. 19, in Dodge Herb.

81. USNEA BICOLORATA Motyka, Lich. Gen. Usnea Stud. Monog. 336. 1937.

Type: Congo, Eastern Province, Kivu Mts., *de Witte.*

Thallus subpendent, 12 cm. long, rigid, pale ashy olive green, irregularly red-spotted; base quite slender, rigid, blackened, slightly attenuate, infrequently sympodially branched almost to the summits, axils 90° or nearly so; branches up to 2 mm. in diameter, rather uneven in thickness, slightly attenuate at the base, abruptly so at the summits, irregularly curved, rarely deeply cracked; more or less terete, indistinctly deformed, and slightly foveolate, papillae obtuse, concolorous, tubercles forming soralia in the upper portion of the thallus, soralia relatively broad, white-farinose, becoming eroded; ramuli quite close, of variable length, similar to branches from dichotomies; summits indistinct, dense. Apothecia not seen.

Our plants from Cameroons are tangled with *Usnea speciosa* and *U. hispida.* They are nearly all Vandyke brown to Natal brown on the main axes although under 12× mignification small patches of citrine drab and dark olive buff are visible and the broken cortex is red-maculate; the medulla is as thick as the axis; otherwise they agree with the above description translated from Motyka. In *Bally B4947*, the soralia are apotheciiform, up to 0.5 mm. in diameter, wider than the branches which bear them.

CAMEROONS: Victoria, in Meyer Crater, 2580 m., on *Aquaria salicifolia, T. D. M. 017 p. p. min.*, ex hb. Bot. Gard. Victoria, at Kew.

KENYA: Mau forest, Endabarrá, 2355 m., on trees at edge of *Acacia* grove forest, *P. R. O. Bally B4947*, glued to sheet of *U. aequatoriana* Motyka, at Kew.

82. USNEA SPILOTOIDES Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Kenya, Chyulu hills, *H. D. van Someren,* in East African Herb.

Thallus probably procumbent, perhaps pendent, subrigid, about 10 cm. long, russet below, shading through tawny to zinc orange and ochraceous salmon, with smaller ramuli pale olive buff; base not seen; branching sympodial or very closely

dichotomous in basal portion where axes are up to 0.9 mm. in diameter, tapering to short subcapillaceous summits, irregularly dichotomous above, some internodes long, others quite short, axils nearly 90°; branches very flexuous, summits mostly recurved, articulate, joints slightly inflated, ends constricted, very variable in length, rarely the cortex regenerating to form very short, darker joints up to 0.3 mm. long, but usually joints separated by a narrow crack; minutely white verrucose, producing single or very few isidia; ramuli very irregularly disposed, sometimes very close, 4 (–10) mm. long, very fragile, slightly verrucose, producing isidiose soredia, becoming minutely farinose as the soredia are shed; ramuli on more slender branches subdistant, about 1 mm. long, smooth, tips acute with long nude areas; summits mostly broken off, up to 20 mm. long, slender, tips acuminate, some nude, others very sparsely short ramulose.

Cortex 55–80 μ thick, of yellow conglutinate thick-walled radial hyphae 7–8 μ in diameter, lumen 1 μ; algal layer 40 μ thick, of protococcoid cells up to 12 μ in diameter, dying in places; medulla 75 μ thick, the outer 35 μ of predominantly periclinal, thick-walled hyphae 5–6 μ in diameter, lumen 3 μ, forming a pseudoparenchyma, the inner 40 μ of slender, densely woven thick-walled hyphae, heavily nubilated with minute brown crystals; axis 650 μ in diameter, solid, of longitudinal, conglutinate thick-walled hyphae 4–5 μ in diameter, lumen 3 μ.

This species belongs in the group with *U. erubescens* and *U. spilota*. Perhaps some of the material referred by Motyka to the latter species may belong here, as Motyka states that the collections from South Africa are "minus certa" and one "juvenilia, possibile ad *U. horridulam* non evolutam spectantia." *U. horridula* differs from *U. spilotoides* in its non-articulate, more regularly ramulose thallus with the isidiose soredia confined to upper parts of the ramuli.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.

83. USNEA MEYERI (Stein) Motyka, Lich. Gen. Usnea Stud. Monog. 338. 1937.
Usnea cornuta v. *Meyeri* Stein, Jahresber. Schles. Ges. Vaterl. Cultur 66:134. 1888.

Type: Tanganyika, Kilimanjaro, 4000 m., saxicole, *H. Meyer*.

Thallus 4–6 cm. tall, erect, very rigid, greenish-stramineous, reddish-maculate, main axes becoming Van Dyke brown, slender branches and ramuli clay color to cinnamon buff, summits nearly white from soredia in the herbarium; holdfasts of radiating, closely branched rootlets, spreading over the surface of the rock and penetrating between the crystals; base about 10 mm. tall, 2 mm. in diameter, cortex annularly cracked and areolate; about thrice dichotomous with very short internodes (appearing polychotomous), each axis with a long internode (10 mm. or more) then again densely branched, the branches terete, curving upward to form a depressed hemispheric tuft; the lowest internode about 2 mm. in diameter, thinning at each dichotomy, the ultimate branches still about 1 mm. in diameter; the lower two internodes blackened, the upper branches clay color to cinnamon buff, testa-

ceous-maculate; surface smooth or low-tuberculate, forming soralia of black-tipped isidiose soredia becoming confluent on some of the ultimate branches; ramuli very irregularly distributed, absent on some branches, subdistant on others, about 2 mm. long, annularly cracked at the base, slightly inflated, tapering to an obtuse tip, some up to 5 mm. long, slightly tuberculate and occasionally forked (perhaps young secondary branches). Apothecia not seen.

Cortex 100 μ thick, so blackened that structure is not clear; algal layer about 60 μ thick in discrete colonies of *Trebouxia* (mostly disintegrated, leaving regularly spaced lacunae just under the cortex, with an occasional cell or small colony remaining; medulla about 160 μ thick, of mostly periclinal thick-walled hyphae about 3 μ in diameter, axis 1000 μ in diameter, solid, of longitudinal conglutinate hyphae interlaced with strands of transverse hyphae.

KENYA: west slope of Mt. Kenya, on trail from West Kenya Forest Station to summit, 3630 m., in giant heath zone, *Edgar A. Mearns 1521, 1536* (T. Roosevelt Exp.), at Farlow Herb.

83a. Var. CHONDROCLADA (Steiner) Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.
Usnea chondroclada Steiner, Verhandl. Zool. Bot. Ges. Wien 53:228. 1903.

Type: Cameroons, Fako, 3600–3800 m., on lava blocks, *Alfred Bornmueller.*

Thallus 4–6 cm. tall, erect, rigid, axes Sayal brown shading to light brownish olive, ramuli Isabella color, indistinctly reddish-maculate; holdfast broken off, base black, 5 mm. tall, 1 mm. in diameter below, expanding to 2 mm. just below the first dichotomy; repeatedly dichotomous just above the base, then sparingly so above; branches 1.3–1.5 mm. in diameter, annularly cracked, not inflated below, slightly so above, thinning somewhat at each dichotomy, slightly verruculose, some verrucae growing out as small ramuli; secondary branches slender, up to 0.6 mm. in diameter, paler and some more clearly reddish-maculate; ramuli from less than 1 mm. to 5 mm. long, slightly inflated, tips acuminate, blackened; the smaller ramuli easily break off leaving minute white scars and probably serve as isidia, especially in the upper portions of the smaller secondary branches and the obtuse summits. Apothecia not seen.

Cortex 65 μ thick, fastigiate, gelified, outer 15–30 μ dark brown, algal layer about 30 μ thick, of *Trebouxia,* cells 7–8 μ in diameter; medulla 100 μ thick, densely woven under the algal layer, looser next the axis, hyphae 3 μ in diameter, lumen about 1 μ; axis solid, about 300 μ thick, of longitudinal conglutinate hyphae interlaced with strands of transverse hyphae.

CAMEROONS: Cameroon Mt., *Alfred Bornmueller* sub *U. chondroclada* f. *ramillosa* Steiner, herb. nom. ? com. Zahlbruckner, in Howe herb. at Farlow Herb.

84. USNEA MACULATA Stirton, Scottish Nat. 6:293. 1882.
Usnea Flotowii v. *subhispida* Zahlbr., Bot. Jahrb. [Engler] 6:541. 1926.

Type: S. Africa, Cape of Good Hope, Somerset East, *P. MacOwan & J. M'Lea,* in Art Galleries of the Glasgow Corporation.

Thallus erect, fruticose, up to 7 cm. tall, pale greenish drying pecan brown to vinaceous tawny (under low magnification spotted with deep olive buff); holdfast a black disc up to 10 mm. in diameter, composed of closely woven rooting fibers giving rise to erect axes, mostly unbranched below, some dichotomous just above the holdfast, blackened for 2–5 mm. at the base, sparingly unequally dichotomous in the upper portion; axes forming a dense erect tuft 10–40 mm. in diameter; subarticulate, joints relatively long and slightly constricted at the ends, up to 1.6 mm. in diameter a short distance above the base, more slender above; surface rather closely tuberculate to subpapillate, papillae either single or concrescent in short irregular ridges, some growing out as caducous, conical spinules about 0.5 mm. long, a few growing out as fragile ramuli, 5–10 mm. long, the larger annularly cracked with obtuse tips, curved, ascending; scars from fallen spinules and smaller ramuli resembling small farinose soralia.

Apothecia sessile on smaller branches, 3–4 mm. in diameter, cupulate; exciple citrine drab to deep olive buff, smooth to slightly tuberculate near the base; marginal cilia dense, up to 5 mm. long, coarse, annularly cracked, slightly constricted at the base, tips obtuse, many broken off; disc concave, somewhat deformed, coarsely cream buff-pruinose.

The apothecia of our plants are apparently young and agree with those described by Motyka for *U. subflorida* (Zahlbr.) Motyka except those of the latter are terminal instead of lateral. The vegetative portion of the plants agrees with that of *U. maculata.* Perhaps when a fuller series of specimens is available, it will be necessary to unite *U. subflorida* with *U. maculata.* Some of our plants are from farther north than either species has been reported. *Greenway 6532* is very young, about 1 cm. tall and sterile, but probably should be referred here.

SUDAN: Mt. Kinelli, 3360 m., on pole and cairn, *T. F. Chipp 64,* at Kew.

UGANDA: Ruizi River, 1390 m., on trees in riverine forest, *T. Jarrett 402 p. p.,* at Kew.

TANGANYIKA: S. Pare Mts., Mt. Mtonto, 2100 m., ramulicole, *P. J. Greenway 6532,* at Kew.

SOUTH AFRICA: without locality, *Drège,* ex herb. W. Sonder sub *U. fragilis* Laurer, herb. nom.?, in Tuckerman herb. at Farlow Herb.

MADAGASCAR: Imerina, Andrangoloaka, *Hildebrandt 2173,* Nov. 1880, com. C. Rensch ex herb. Sbarbaro sub *U. barbata* v. *scabrosa* (Ach.) Müll. Arg., at Farlow Herb.

85. Usnea acanthera Vainio in Motyka, Lich. Gen. Usnea Stud. Monog. 358. 1937.

Type: S. Africa, Bechuanaland, Crocodile River, *Klingsberg,* in Riksmuseet, Stockholm.

Thallus prostrate to suberect, rigid, about 6 cm. long, ashy green, darker on the main axes; divaricately dichotomous just above the base and sparingly so below the summits; axes 1 mm. in diameter, sigmoid-curved, continuous, terete, surface uneven, not papillate although very young ramuli may simulate papillae; ramuli dense, strigose, perpendicular, about 2 mm. long, pale green, smooth.

Apothecia terminal, up to 7 mm. in diameter, almost plane; exciple slightly uneven or rugose, densely ciliate; marginal cilia dense, 4–5 mm. long; disc subplane, margin often broken, flesh color, almost epruinose; epithecium fusco-fuligineous; ascospores 6 × 9 μ in narrow asci.

Cortex 30 μ thick, chondroid, pale green; medulla 120–140 μ thick, rose color, dense, K—; axis 360 μ in diameter, white with narrow central cavity, slightly spotted with a few black hyphae.

Our specimens seem to be juvenile forms of this species. The branching is dense at the woody base, 4 mm. in diameter, 5 mm. tall, only once dichotomous above in about the middle of the axis, branches nearly straight; ramuli 3–5 mm. long; summits slender, the uppermost 10 mm. eramulose. Sterile but not sorediose in the Kenya specimen, a few very young apothecia present in the Uganda specimen.

KENYA: Chyulu hills, *H. D. van Someren*, in E. African Herb.
UGANDA: Kigezi, Mafuga, 2410 m., *I. R. Dale L41 p. p. min.*, at Kew.

86. USNEA MAROCANA Motyka, Lich. Gen. Usnea Stud. Monog. 359. 1937.

Type: Maroc, Camp Monod, arboricole, *Mouret*.

Thallus 5–8 cm. tall, fruticose, pale ashy green, drying deep olive buff to olive buff; dichotomous just above the holdfast and twice or thrice dichotomous below with rather short internodes and once or twice dichotomous at the summits; nearly terete with occasional low ridges where the ramuli are close in rows; branches mostly 1.2–1.3 mm. in diameter in the lower three fourths of their length, then tapering upward to slender acute summits; surface smooth except for young ramuli or isidia; ramuli rather close, tending to form vertical rows, bases of the larger ramuli somewhat complanate, the smaller less so; mostly 5–10 (–15) mm. long, often annularly cracked just above the base, slightly inflated in the middle and tapering to acute tips, mostly smooth below, verrucose and isidiose above, the verrucae appearing minutely farinose after the isidia are shed.

Cortex 65–90 μ thick, probably fastigiate but so gelified as to appear structureless; algal layer continuous, 30–40 μ thick, of *Trebouxia*, cells 5–6 μ in diameter, with some colonies invading to the middle of the cortex; medulla pinkish, compact, about 130 μ thick, of thick-walled interwoven hyphae; axis about 1100 μ in diameter, appearing solid, but lacerate with scattered small cavities about 10 μ in diameter.

SIERRA LEONE: Gebense, Sefadu, on trunk of *Elaeis guineensis*, *F. Adames*, com. *F. C. Deighton M4756*, at Kew.

87. USNEA AMPLISSIMA Stirton, Scottish Nat. 6:106. 1881.

Usnea arthroclada subsp. *arthrocladodes* Vainio, Cat. Welwitsch's African Pl. 2:397. 1901.

Type: S. Africa, Cape of Good Hope, Somerset East, *P. MacOwan*. Type of *U. arthroclada* subsp. *arthrocladodes* Vainio is: Angola, Golungo Alto, Serra do Alto Queto, *Welwitsch 69 p. p.*; both in British Mus.

Thallus about 60 cm. long, pendent, very rigid, ashy or pure green, partly paler and very slightly reddish; base very large and firm, infrequently but several times dichotomous, axils 90°, branches arcuate, pendent, of nearly the same diameter throughout, up to 2.5 mm. in diameter, tapering slightly at the ends, neither exactly terete nor clearly angled; surface uneven, irregularly subareolate, closely annularly cracked, the cortex regenerating at the cracks, paler or pinkish, wherefore the surface appears irregularly rugose and scabrous on account of the areolation and the coarse concolorous tubercles; ramuli close, slightly curved, very thick at the base, tapering gradually to the tips, the thicker ones tuberculate and sometimes branched, the more slender ones smooth, tips obtuse, closely annularly cracked and subulate.

Apothecia abundant, usually at the tip of a lateral branch, 10–20 (–30) mm. in diameter, nearly plane; exciple smooth (subfoveolate on very large apothecia); marginal cilia not dense, radiating, about as long as the diameter of the disc, usually not branched, annularly cracked, tips acuminate, usually smooth but some of the longer ones slightly tuberculate; disc plane or slightly rugose in the larger apothecia, dirty flesh color, slightly pruinose; thecium about 70 μ tall, epithecium greenish fuliginous, ascospores 11 $\times$ 7 μ in slightly inflated asci.

Cortex about 100 μ thick, chondroid, but soft, fragile, green with reddish spots; medulla about 180 μ thick, white, dense, K—; axis about 500 μ thick, white.

The above description is translated from Motyka as our specimens are rather young, only about 15 cm. long and sterile. The cortex is areolate but not slightly rugose. Since no suggestions of soredia on the tubercles have been seen, it is possible that our material may be young *U. distensa*; however, in our younger plants of that species, about the size of the present plants, soredia have already developed. The specimen from Kenya is only a fragment from the middle of the thallus but it is abundantly fertile.

KENYA: western slope of Mt. Kenya along trail from West Kenya Forest Station to summit, 3630 m., in giant heath zone, *Edgar A. Mearns 1533* (T. Roosevelt Exp.) ex G. K. Merrill herb., at Farlow Herb.

ANGOLA: Cuanza Sul, Amboim, Capir near the Carloaongo-Cuvo River, 1000 m., *J. Gossweiler 9991*, at Kew.

88. USNEA DISTENSA Stirton, Scottish Nat. 6:104. 1882.

Type: S. Africa, Cape of Good Hope, Griqualand West, Kimberley Diamond Fields, *T. Shaw*, in Art Galleries of the Glasgow Corporation.

Thallus pendent, rigid, up to 70 cm. long (only 15 cm. in the type), green, drying deep olive buff; holdfast up to 8 mm. in diameter, blackened, base 2 mm. in diameter, about 10 mm. long, closely annulate, blackened for a variable distance in different plants, then closely dichotomous above the base (axils 90°) and less frequently and more irregularly so above; main axes about 1.5 mm. in diameter, thinning at each dichotomy to the capillaceous tips (about 6–10 cm. long), closely

annulate and subareolate on the main axes, smooth with a few minute pale tubercles, becoming more and larger tuberculate on the more slender branches, sometimes somewhat foveolate and angled; sparingly and irregularly ramulose on some main axes, quite closely so on others; ramuli about 25 mm. long, closely tuberculate, forming soralia of isidiose soredia, the more slender branches more regularly and closely ramulose, the ramuli shorter, 5–15 mm. long, more slender and less tuberculate, all ramuli rather fragile. Apothecia not seen.

Our Central African material is rather short, mostly about 30 cm. long, and may represent young plants although abundantly sorediiferous. The main axes are not subscrobiculate from regenerating cortex of the fissures; otherwise it agrees well with Motyka's description.

UGANDA: Mt. Elgon, 1290 m., on trees, *W. Small 218* (fragments from terminal portions of the thallus).

TANGANYIKA: Usambara, Amani, 1000 m., in rain forest, *P. J. Greenway 998*, in E. African Herb. and at Kew; Amani-Maramba, 1030 m., *P. J. Greenway 4151*, in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, Griqualand West, Kimberley Diamond Fields, *T. Shaw*, in Art Galleries of the Glasgow Corp.; Cape of Good Hope, Knysna, on *Quercus*, *O. Almborn*, Lich. Afric. 18, in Dodge Herb.

CONGO: km. 30, route Kahusi, *F. L. Hendrickx 4330*, in E. African Herb.
18, in Dodge Herb.

MAURITIUS: without locality or collector, ex herb. Macreight in Tuckerman herb. sub *U. plicata*, at Farlow Herb.

89. USNEA PROMONTORII Motyka, Lich. Gen. Usnea Stud. Monog. 386. 1937.

Type: S. Africa, Cape of Good Hope, in primeval forest, *Rehman*.

Thallus pendent, quite rigid, more than 100 cm. long, pale ashy green (Motyka) drying chamois to cream buff in our material; base not seen; branching dichotomous, axils usually 90°, complanate, the branches curving downward until the axes are nearly parallel, internodes very long, subflexuous to straight, the ultimate 20 cm. unbranched, about 1 mm. in diameter below, tapering to the long slender tips; cortex of main axis coarsely areolate, margins of areoles slightly elevated, giving a rough, subrugose appearance, the more slender portions with scattered low, pale tubercles, often in somewhat oblique rows, perhaps giving rise to small soralia but not present in our South African material (a few in our Kenya specimens); ramuli irregularly disposed, sometimes quite close, in other places subdistant, fragile, 5–15 (–20) mm. long, curved, axils not complanate, slender, tapering to acuminate tips.

Except for greater length and color, our plants agree closely with Motyka's description.

CONGO: Mt. Kahusi, 2700 m., *F. L. Hendrickx 4316*, basal fragment only, in E. African Herb.

KENYA: Mau forest, Endabarra, 2030 m., in *Acacia* shrub forest, *P. R. O. Bally B4947*, in E. African Herb.

SOUTH AFRICA: Cape of Good Hope, Knysna District, Hermansdorp Division, on

branches of *Podocarpus Thunbergii, A. W. Woodcock,* ex hb. Mus. Austro-Africanum, at Kew.

MAURITIUS: without locality, *Sieber 43,* in Tuckerman herb. sub *U. plicata,* at Farlow Herb.

90. USNEA GONIODES Stirton, Scottish Nat. 6:108. 1881.

Usnea angulata f. *goniodes* Hue, Nouv. Arch. Mus. Paris, IV. 1:45. 1899, *quoad nomen sed non descriptio.*

Type: South Africa, Cape of Good Hope, *H. Bolus 517,* in Art Galleries of the Glasgow Corporation. Hue based his new combination on a plant from Paraguay, Peribebuy, *Balansa 4140,* probably *U. sulcata* v. *neutra* Motyka, from his description.

Thallus pendent, subrigid, about 30 cm. long, green, drying deep olive buff (finally sayal brown to snuff brown in the type); holdfast a dark disc about 2 mm. in diameter, on the upper side of a twig from which two or more axes arise, 0.5–0.7 mm. in diameter, about 2 cm. long, cylindric, annulate with very few ramuli, curving over either side of the twig, then dichotomous and becoming triangular in cross-section; cortex irregularly annular and subareolate, ridges usually corticate, sometimes cracked, up to 1.2 mm. in diameter (only 0.8 mm. in our rather young material), very rarely dichotomous above; axes flexuous and subparallel throughout, thinning gradually to the very slender, almost cylindric filiform summits; ramuli from the ridges, bases complanate, quite close, mostly about 10 mm. long, very slender, an occasional one growing out as a very slender lateral branch up to 50 mm. long, with small ramuli, the larger ramuli tuberculate and sometimes isidiose sorediose.

Apothecia up to 15 mm. in diameter, at the tips of lateral branches, plane; exciple slightly to deeply rugose-reticulate and sublacunose, epapillate; marginal cilia few and often missing, up to 10 mm. long, tuberculate; disc plane, distinctly rugose, flesh color, chalky, pruinose (olive buff in type and in *Brass 16992*).

Cortex 55–65 μ thick, fastigiate, of very thick-walled, conglutinate hyphae, the outer 20 μ slightly brownish; algal layer 25 μ thick, of closely packed cells of *Trebouxia* 6–8 μ in diameter; medulla about 130 μ thick, of densely woven thick-walled hyphae, heavily nubilated with dark brown minute crystals, more loosely woven about 40 μ outside the axis and tearing on sectioning; axis 730 μ thick, appearing solid but minutely lacerate with many small cavities about 10 μ in diameter in the inner three fourths of the axis, of thick-walled hyphae 6–8 μ in diameter, lumen 3 μ.

Some of our material is young and sterile. In several places, some injury to the cortex has been followed by a dense branched tuft of ramuli. *Gossweiler 13654* consists of a few fragments as if broken from the middle of the primary axes, or perhaps younger plants; *Brass 16992* is a fragment from the terminal portion of the thallus, fertile, quite typical except that the soredia are less developed than in the type.

ANGOLA: nordeste de Lunda, Dundo near Rio Luachimo, 700 m., *J. Gossweiler 13654.*

NYASALAND: Mt. Nchisi, corticole, *L. J. Brass 16992* (Vernay Nyasaland Exp., 1946), in N. Y. Bot. Gard. Herb.

PORTUGESE EAST AFRICA: without locality, *J. Stocks 39*; Mozambique, Inhambane, on *Copaifera,* without collector, a fragment separated from material of *U. trichodoides* Vainio; both at Kew.

SOUTH AFRICA: Cape of Good Hope, *H. Bolus 517,* type in Art Galleries of the Glasgow Corporation; Adelaide, *Miss Brugton,* com. Rev. W. Lillie, in Howe herb., det. *U. angulata* by M. Bouly de Lesdain, cited by Motyka (Monog. p. 397), at Farlow Herb.

91. USNEA CHLOREOIDES (Vainio) Motyka, Lich. Gen. Usnea Stud. Monog. 397. 1937.

Usnea angulata f. *chloreoides* Vainio, Hedwigia 37:40. 1898.

Type: Uganda, near Mt. Ruwenzori, Nzowi Nez, 0° 5′ S., *Scott-Elliott.*

Thallus pendent, subrigid, about 50 cm. long, between citrine drab and deep grape green; base not seen; frequently dichotomous, branches somewhat flexuous, quite uniformly 1.2 mm. in diameter, frequently and irregularly transversely cracked, angulate, the ridges formed of coalescent rows of coarse papillae, many of which develop into ramuli, with occasional tubercles between, axis not conspicuously sulcate, some ridges quite high and almost alate; ramuli dense, very fragile, annularly cracked, tuberculate, 3–6 mm. long, tapering upward but tip obtuse and slightly brownish.

Apothecia absent in the type, abundant in our plants, up to 10 mm. in diameter, lateral on short lateral branches about 0.3 mm. in diameter, stalks coarsely papillate, not angled, quite fragile; exciple deeply incised, margin lobed, smooth, nearly plane; marginal cilia few, 1–3 mm. long, conical, quite fragile; disc plane, vinaceous cinnamon, slightly pruinose when young.

Under two of the apothecia, the branch has grown out beyond the apothecium for 7 cm., about 0.5 mm. in diameter. With some hesitation I have referred our fertile coastal lowland material to a sterile species from the highlands of Mt. Ruwenzori. The thallus agrees quite well with Motyka's description, except for more abundant and shorter ramuli and more alate ridges, the upper portion of which often break away, leaving long white scars.

KENYA: Tana River, 16 m., on trees, *E. Battiscombe 227,* at Kew.

PORTUGESE EAST AFRICA: Lourenço Marques, *Cecil P. Cross,* ex herb. G. K. Merrill, at Farlow Herb.

MADAGASCAR: Fort Dauphine, *native collector,* com. F. G. Paris ex herb. H. E. Hasse, at Farlow Herb.

92. USNEA FERNANDIAE Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:110. 1952.

Type: Congo: Bas-Congo, Ngombe-Matadi, *Paul Duvigneaud 305 U3,* in Herb. Duvigneaud, portion of type in Bot. Mus. Lund., loaned by Dr. Ove Almborn.

Thallus pendent, subrigid, 70 cm. or more long, flexuous, grayish green; primary holdfast not surely seen, but secondary holdfasts formed where lateral branches come in contact with a twig, consisting of discrete, radiating rooting fibers forming a disc 1 mm. in diameter; secondary bases terete, of variable length, cortex smooth, subannularly cracked; irregularly dichotomous at nearly right angles but the branches soon curving downward and subparallel, axils slightly complanate; branches mostly 4- to 5-angled with low obtuse ridges, occasionally acute but not alate, from concrescent rows of tubercles, scars of minute fallen spinules and the complanate bases of ramuli, but in some places almost terete, plane or slightly convex between the ridges, irregularly annularly cracked; slender lateral branches perpendicular to the main axes, terete, 20–40 mm. long, 0.4–0.6 mm. in diameter, sparingly ramulose, minutely tuberculate from scars of fallen spinules, abruptly tapering to acute tips which are sometimes forked; ramuli mostly 5–7 mm. long, about 0.2 mm. in diameter, cortex smooth, rarely annularly cracked above the somewhat complanate base, tips acute but very fragile and mostly broken off; summits more slender and fragile but not very distinct.

Apothecia (absent in specimen available) at tips of slender lateral branches, up to 15 mm. in diameter; exciple smooth; marginal cilia few or none; disc almost plane, white-pruinose.

Cortex 35 μ thick, gelified, fastigiate, outer 6 μ filled with dark brown granules, thinning over the ridges and regenerating in cracks until it reaches the bottom of the algal layer; algal layer about 80 μ thick, of discrete colonies of *Trebouxia* 15–20 μ in diameter, forming a nearly continuous layer on the outside, less close within, cells 6–7 μ in diameter; medulla 80–100 μ thick, densely woven just under the algal layer and next the axis, very lax between, hyphae 3 μ in diameter, lumen less than 1 μ; axis 420 μ in diameter, with two cavities near the center, each about 50 μ in diameter, of longitudinal, thick-walled hyphae 6–7 μ in diameter, lumen nearly 2 μ, with scattered thin-walled hyphae 6–7 μ in diameter, filled with a deep yellow, highly refractive material (oil?), scattered singly or lying side by side in short rows, not radially arranged.

The portion of the axis available for study is younger than that of *U. bakongensis*; perhaps in the older part of the axis, the central cavities coalesce to form a relatively large central cavity as in that species, which it resesmbles in structure of the axis. The medulla is better differentiated and laxer in *U. Fernandiae.*

CONGO: Bas-Congo, Ngombe-Matadi, *Paul Duvigneaud 305 U3*, cotype in Bot. Mus. Lund.

93. Usnea africana Motyka, Lich. Gen. Usnea Stud. Monog. 398. 1937.

Type: Tanganyika, Usambara Muandara forest, C. *Holst.*

Thallus pendent, subrigid, up to 110 cm. long, dark olive buff, ramuli olive buff (from soredia); base absent in our material, frequently dichotomous just above the base, then occasionally so throughout, branches often more or less twisted about

each other (wind action?), branching at right angles, the two branches curving downward below the axil to become almost parallel, somewhat flexuous, the proximal portion up to 1.8 mm. in diameter, tapering evenly to the summits; cortex irregularly transversely and longitudinally cracked, with a few low longitudinal ridges (more in *Eyles 1023*) formed from the complanate axils of the ramuli; ramuli 4–10 (–20) mm. long, densely verrucose with soralia of isidiose soredia, quite fragile, tips acute. Similar soralia from the verrucae are abundant on the more slender portions of the main axes.

T. W. Maitland 396 is doubtfully referred here. It consists of a coarser, more rigid plant, axis 2 mm. or more in diameter, more conspicuously angled and less frequently dichotomous; the ramuli are 20–30 mm. long and thicker. The Kenya plant is also doubtful. It consists of fragments about 10 cm. long, the main axes tawny olive to clay color, the ramuli chamois to cream buff. It seems closer to *U. africana* than to the STRAMINEAE, SULCATAE.

KENYA: uplands, 2250 m., *E. R. V.*, ex Corydon Mus. 5161, at Kew.

UGANDA: Busoga, Jinja, 1590 m., *E. Brown 91*, ex Bot Gard. Entebbe; Mile 8 on Masaba Road, 1130–1240 m., *F. Chandler 1891*, moribund; Bangala, Sese, 1190 m., *T. W. Maitland 396*; all at Kew.

TANGANYIKA: Mpwampwa, Kiboriani Mt., 1770–1930 m., *B. D. Burtt 3880*; Kondoa District, on *Oxyanthus speciosus* DC., *B. D. Burtt 1183*, at Kew.

S. RHODESIA: Matopos, 1610 m., *Frederick Eyles 1023*; Melsetter District (Gazaland), Chimanimani, 2250 m., *C. F. M. Swynnerton 617*; both at Kew.

94. USNEA BAKONGENSIS Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:109. 1952.

Type: Congo: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U2*, in herb. Duvigneaud, portion in Bot. Mus. Lund, loaned by Dr. Ove Almborn.

Thallus pendent, 70 cm. and more long, subrigid, grayish green; primary holdfast broken off in specimen studied, secondary holdfasts fibrous discs 3–4 mm. in diameter, dark brown; secondary base about 1 mm. in diameter, of variable length, cortex annulate and subareolate; main branches 1–1.5 mm. in diameter below, tapering gradually to more closely ramulose, capillaceous summits about 7 cm. long; rather sparingly dichotomous at about 45° angles, the branches slowly curving downward; below nearly terete except for complanate bases of small lateral branches, rather closely annularly cracked, the cracks regenerating as transverse ridges with minute low tubercles producing 1–3 spinules, becoming irregularly angular above from short longitudinal ridges formed by the complanate bases of small lateral branches, or ramuli, and the upturned edges of longitudinal cortical cracks with rows of scars of fallen spinules, closely but incompletely annularly cracked forming transverse ridges as in the lower portion, with scattered scars of fallen spinules between; ridges less conspicuous toward the summits which are terete with rare scars; ramuli mostly broken off below, subdistant, becoming closer above, especially on the capillaceous summits, 5–10 mm. long, the shorter smooth, the longer covered with minute, fragile spinules.

Cortex 65–80 μ thick, gelified, fastigiate, hyphal lumina about 1 μ in diameter, the outer 10 μ heavily nubilated with brown granules; algal layer about 225 μ thick, of discrete colonies of *Trebouxia*, about 25 μ in diameter, forming a nearly continuous layer on the outside with similar colonies less closely packed almost to the axis, the inner 25 μ with only an occasional colony; medulla not differentiated as a distinct layer unless the inner 25 μ of the algal layer be so considered; axis 800 μ in diameter, wall 170–200 μ thick, of longitudinal thick-walled, conglutinate hyphae 3.5 μ in diameter, lumen 1 μ, with thin-walled hyphae 5–6 μ in diameter arranged in nearly continuous, mostly radial rows (suggesting the appearance of rays in transverse sections of coniferous wood), cell contents highly refractive as if filled with an oil or resin, colored deep brownish yellow; central cavity stellate in outline of transverse section, 400–460 μ in diameter, probably formed by the coalescence of 7–8 central cavities, loosely filled with contorted, thick-walled hyphae 6–7 μ in diameter, lumen about 2 μ, nubilated with minute hyaline granules.

In the original description, Duvigneaud states "medulla et axis K lutescentes et dein rubescentes." In the specimen studied, on shaving off the cortex of an upper portion of a main branch and treating with K, a yellow color promptly develops which goes into solution in K, leaving the exposed medulla white when the solution is blotted off. Mounting transverse sections near the base of a main branch in K, all color disappears from the sections except for algal cells.

CONGO: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U2*, in herb. Duvigneaud, portion of cotype in Bot. Mus. Lund.

95. USNEA LIVIDA Motyka, Lich. Gen. Usnea Stud. Monog. 419. 1937.

Type: Cameroons, Mt. Cameroon, *Winkler*.

Thallus 100 cm. long, pendent, flaccid, uniformly ashy green, partly slightly fuscescent (dark olive buff to deep olive buff in our material); base not seen, infrequently dichotomous throughout, branches irregularly flexuous, somewhat contorted, about 0.8 mm. in diameter below, slightly compressed and up to 2 mm. wide where the complanate axils of ramuli are nearly opposite, the more slender portions terete, slightly longitudinally rugose from areolation of the cortex which cracks away in places leaving farinose decorticate areas; ramuli somewhat irregularly disposed with complanate axils on the larger axes, less so on the slender ones, often curved, tips acuminate, sometimes blackened, variable in length, fragile.

Apothecia sessile on short lateral branches or near the base of a large ramulus, 3–4 mm. in diameter, nearly plane; exciple slightly impressed; marginal cilia about 12, very variable in length; disc slightly concave, carneous, densely white-pruinose.

Cortex 40–45 μ thick, highly gelified, the outer 15 μ brownish; algal layer 20–25 μ thick, of discrete colonies of *Trebouxia*, cells 6–8 μ in diameter; medulla 40–55 μ thick, of densely woven slender hyphae, heavily nubilated; axis 670 × 490 μ, outer surface eroded longitudinally, appearing solid, but slightly lacerate

with a few narrow bundles of slightly brownish, coarser hyphae, resembling the rays of vascular plants.

Most of our material is rather young and is densely tangled, somewhat smaller in dimensions than the type, but agrees well in essential characters.

SIERRA LEONE: Sugar Loaf, 480 m., *H. Donovan Tindall 16*, at Kew.
GOLD COAST: C. P., Ashanti, Agogo, 510 m., *T. F. Chipp 445*, at Kew.
CÔTE D'IVOIRE: Gommèlé, Agnibile-Krou, *Guy Roberty 13553*, in Herb. Mo. Bot. Gard.
CAMEROONS: Victoria, in Meyer Crater, 2580 m., on *Aquaria salicifolia*, *T. P. M. 917 p. p. min.*, fragment tangled with *Usnea speciosa* Mot., at Kew.

96. USNEA AMANIENSIS Dodge, Ann. Mo. Bot. Gard. 43:396. 1956.

Type: Tanganyika, East Usambara, Amani-Maramba, 1030 m., growing in festoons on the topmost branches of tall evergreen rain-forest trees, *P. J. Greenway 4151*, ex Herb. E. African Agr. Res. Sta., Amani.

Thallus prostrate and creeping along the larger branches of trees, the more slender branches pendent, rigid, more than 60 cm. long, chamois to deep colonial buff; base black, conic, 5 mm. in diameter, buried in humus (decaying mosses, leaves, etc.) and attached to the bark, tapering upward to 1.4 mm. in diameter and about 10 mm. long, then several times dichotomous with short internodes, then rarely dichotomous throughout; principal axes about 1 mm. in diameter, thinning at each dichotomy to the capillaceous summits; short lateral branches or ramuli penetrate the humus and form secondary holdfasts on the underlying bark, giving rise to secondary axes; terete, smooth, without verrucae or tubercles; main axes closely annularly cracked, the cortex regenerating over the crack, producing a white annular appearance of the larger axes, longitudinal cracks rare and the areoles do not crack off; the more slender branches with very narrow annular cracks, sometimes close, sometimes distant on the same branch, terete or with single minute paler verrucae; ramuli 10–20 mm. long, very slender, straight or curved, rather fragile, tips acute, sparsely and minutely tuberculate, no soredia, isidia nor propagula seen.

Apothecia abundant on some axes, absent on others, 3–5 mm. in diameter, cupulate, becoming subplane, sessile on ramuli, eciliate; exciple smooth; disc fuscous, white-pruinose.

Cortex about 55 μ thick, apparently fastigiate but so highly gelified it is impossible to see the structure clearly; algal layer 45 μ thick, of discrete colonies of *Trebouxia* about 30 μ in diameter, forming a nearly continuous layer; medulla 105–120 μ thick, of very densely woven hyphae, so heavily nubilated with minute brown crystals that structure is not very clear; axis 450 μ in diameter, of strands of longitudinal, conglutinate hyphae, lumen 1–1.5 μ in diameter, separated by thin-walled hyphae 6–8 μ in diameter very heavily nubilated with brown crystals (giving a brown reticulate appearance to the transverse section).

The Nyasaland fragment has a single apothecium 9 mm. in diameter, a slightly thicker cortex; the axis appears solid, i. e. the thinner walled cells have not yet

turned brown and are not nubilated. The color of *U. amaniensis* is suggestive of the GLABRATAE, OSSEOLEUCAE, but all the other characters clearly relate it to the ELONGATAE, CERATINAE or LONGISSIMAE.

TANGANYIKA: East Usambara, Amani-Maramba, 1030 m., growing in festoons on the topmost branches of tall evergreen rain-forest trees, *P. J. Greenway 4151*, ex Herb. E. African Agr. Res. Sta. Amani.

NYASALAND: Mlanje District, Luchenya Plateau, Mt. Mlanje, 1890 m., *L. J. Brass 16845, 16828, fragment* (Vernay Nyasaland Exp., 1946), in N. Y. Bot. Gard. Herb.

97. USNEA EBURNEA Motyka, Frag. Flor. Geobot. 1:29. 1954.

Type: Madagascar, Manakambahiny Est, large wood between Alaatra and Tamatave, near Saharakara River, 800 m., com. *H. des Abbayes.*

Thallus pendent, quite rigid, about 80 cm. long, yellow-stramineous (cream buff in our plant); holdfast a black disc 5 mm. in diameter, surface with radial ridges (coalesced rooting fibers), base 2–3 mm. long, closely annulate, dichotomous at very obtuse angles, soon dichotomous at a 90° angle and occasionally so above with long internodes, axes quite flexuous, very slightly angled, almost terete, rarely with cristate ridges on larger branches, closely annular, terete on more slender branches and less closely annulate; surface with scattered subpapilliform tubercles, sometimes in irregular rows on the larger branches, apparently elongating and breaking off as a rather stout isidium, paler than the thallus; ramuli close except near the base, mostly 10 (–20) mm. long, curved, tapering to an acuminate point, minutely and sparsely tuberculate.

Apothecia not abundant (absent in our material), subterminal on larger ramuli, 2–4 mm. in diameter, concave becoming plane or even revolute, deformed; exciple smooth, eciliate; disc deep flesh color, white-pruinose.

MAURITIUS: without locality or collector, at Kew.

98. USNEA SAVANARUM Duvigneaud, Bull. Soc. Roy. Bot. Belg. 85:112. 1952.

Type: Congo: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud, 582 U4,* in Herb. Duvigneaud, two fragments in Bot. Mus. Lund, loaned by Dr. Ove Almborn.

Thallus pendent, 50 cm. or more long, flaccid, grayish green; holdfast and base not seen; primary axes somewhat flexuous, 0.5 mm. in diameter, subterete, occasionally subangular from slightly elevated isidial scars in rows; surface subareolate-corticate (not scaling in the material studied, perhaps so in the lower portion of the thallus) appearing decorticate from coalescent scars of fallen isidia and minute spinules up to 0.3 mm. long, partly tartareous from protruding medullary hyphae; ramuli 3–5 mm. long, perpendicular, abruptly tapering to acute tips, close, smooth or nearly so, about twice annularly cracked; slender short lateral branches up to 25 mm. long, unequally dichotomous, minutely spinulose, appearing minutely

farinose-tuberculate after the spinules are shed.

Apothecia (absent in specimen studied) 3–4 mm. in diameter; exciple sub-smooth to very slightly pitted; marginal cilia few, resembling the ramuli; disc white.

Cortex about 40 μ thick, fastigiate, hyphae 6–7 μ in diameter, lumen 1 μ, gelified, the outer 10 μ heavily nubilated with dark brown granules; algal layer of discrete colonies of *Trebouxia*, about 15 μ in diameter, forming a nearly continuous layer, with some colonies much deeper in the medulla; medulla 30–35 μ thick, of rather densely woven, predominantly radial hyphae, 6–7 μ in diameter, laxer next the axis, heavily nubilated with dark brown crystals, soluble in KOH but not in lacto-phenol; axis solid, brownish, 250 μ in diameter, of conglutinate, longitudinal hyphae, about 4 μ in diameter, lumen about 1 μ; axis K reddish brown; medulla K yellow becoming orange as the solution dries. Transverse sections are promptly bleached by K except for the algal cells.

Occasionally a member of a dichotomy of a short lateral branch is very densely branched, forming a compact cluster 3–4 mm. in diameter, probably teratological. Only two fragments about 10 and 12 cm. long, were available for study. These are clearly from the upper half of a main branch and are clearly corticate throughout, but it is probable that the basal portion of the thallus would show some scaling, due to the thin, laxly woven region of the medulla next the axis.

CONGO: Bas-Congo, between Thysville and Tumba, *Paul Duvigneaud 582 U4*, cotype fragments in Bot. Mus. Lund.

99. Usnea indigena Motyka, Frag. Flor., Geobot. 1:27. 1954.

Type: Madagascar, Manakambahiny Est, large wood between Alaatra and Tamatave, Sahamalaza, 800 m., com. *H. des Abbayes.*

Thallus pendent, flaccid, about 30 cm. long, chamois to cream buff; dichotomously branched, the branches curving downward until they are soon nearly parallel as main axes, 0.7–0.8 mm. in diameter, subsequent dichotomies rare, axils complanate, 90°; very indistinctly few-angled, lower portion of axes annulate, smaller branches continuous, terete, smooth, tapering to capillaceous summits; ramuli moderately close throughout, slender, tapering to acuminate tips, mostly 4–10 mm. long, a few longer and dichotomous at their tips, bearing a few minute spinules which break away and serve as isidia.

The ramuli are capable of forming a holdfast where they come into contact with a twig, as a black disc about 1 mm. in diameter.

NYASALAND: Mt. Mlanje, on Likabula Valley track, 1610 m., in *Podocarpus-Widdringtonia* forest on steep rocky slopes, *P. J. Greenway 6332*, ex hb. E. African Agr. Res. Sta., Amani 374/46, at Kew.

MADAGASCAR: Cercle M. des Merie [? illegible], *native collector*, vere 1901, ex herb. H. E. Haase, at Farlow Herb.

100. Usnea contorta Jatta, Malpighia 19:163. 1905.

Type: Madagascar, Piunarantsoa, Beforna, collected by a native.

Thallus pendent, subflaccid, up to 60 cm. long, pale stramineo-green (Motyka), dark olive buff to deep olive buff in our plants; holdfast a thick black disc 5 mm. in diameter, base blackened, 5 mm. long, 1 mm. in diameter, closely annulate, branching closely dichotomous just above the base, axils sometimes complanate, the branches curving and becoming subparallel, very rarely branched above, often one branch larger than the other; axes 1 mm. in diameter, areolate below, sometimes with simple cracks, in other plants the margins of the areoles obtusely elevated, subscrobiculate with predominantly oblique ridges, giving a somewhat contorted appearance, rarely low-tuberculate between as well as on the ridges, more slender branches closely but indistinctly annulate with scattered single tubercles; ramuli irregularly disposed, rare on the lower portions of the main axes, closer above but not crowded, 10–20 (–35) mm. long, faintly tuberculate, some straight, others curved or flexuous, tapering uniformly to acuminate, slightly darkened tips.

Apothecia not abundant, sessile on the more slender portions of a main axis, or more frequently lateral in the middle of a very long ramulus, cupulate, becoming plane; marginal cilia irregularly disposed, quite close, erect, of variable length, similar to ramuli; exciple smooth, margin splitting and becoming crenate; disc pale flesh color, white-pruinose (in some, the thecium has been eaten away by insects and small erect cilia develop on the old disc).

tanganyika: Southern Highlands, Iringa District, Morgana, 1930 m., *W. Carmichael 296,* in E. African Herb.

south africa: Uitenhage District in forest, *Ecklon,* ex herb. W. Sonder, in Tuckerman herb. at Farlow Herb.

mauritius: without locality, *Robillard* ex Gray Herb. at Farlow Herb.

réunion: Salazie, *Frère Rodriguez,* com. Bouly de Lesdain ex herb. Hasse sub *U. mascarena* Motyka olim herb. nom., at Farlow Herb.

101. Usnea arguta Motyka, Lich. Gen. Usnea Stud. Monog. 406. 1937.

Type: Congo, Congo de Lemba, *Goliat.*

Thallus up to 40 cm. long, rather more rigid than *U. trichodeoides,* pendent, axes pale olive buff when decorticate with isidiose soredia, corticate portions and ramuli olive buff; base not seen; infrequently dichotomous with obtuse axils, the branches curving downward and soon parallel; axes about 1 mm. in diameter below, somewhat flexuous, terete to slightly longitudinally rugose, cortex cracking off and then farinose with abundant isidiose soredia, patches of cortex remaining with minute sorediose verrucae; ramuli quite close, 10–20 (–30) mm. long, the longer subdichotomous, tips acuminate, straight or curved, corticate with minute, irregularly disposed pale tubercles, forming soralia on the longer ramuli, but never as dense as on the axes.

Apothecia (on *Chipp 57* only) sessile on the smaller branches, up to 6 mm. in diameter, nearly plane; marginal cilia few, radiating, 5–10 mm. long, similar to

ramuli; disc flesh color, white-pruinose, becoming nude when old.

Our plants are mostly short fragments about 20 cm. long, but agree with Motyka's description. Perhaps the variable amount of decortication may be correlated with habitat, depending on dryness and wind. Plants referred here from semi-swamp, dense forests are much more corticate than from open scrub woodland and savannas. *Eyles 1023*, a short fragment from the mid-portion of a main axis, is somewhat doubtfully referred here. The axis is mostly corticate and more distinctly rugose than the other plants, but much less so than in *U. aequatoriana* Mot. Curious spinules with dark tips are irregularly borne on some ramuli.

SUDAN: Issore, Onyiro, 3° 50′ N., 32° 50′ E., 1720 m., *T. F. Chipp 57*, more corticate and fertile, at Kew.

KENYA: Chyulu hills, 1290 m., on trees in mixed savanna forest on lava flows, *P. R. O. Bally 1236*, at Kew.

UGANDA: Ruizi River, 1390 m., in riverine forest, *T. Jarrett 402 p. p.*, at Kew.

TANGANYIKA: Bukoba, Kabobwa, Mingiro Forest Reserve, 1550 m., on trees of dense semi-swamp evergreen forest, *G. Watkins 492* (native name: *machankima*), at Kew

N. RHODESIA: E. Isoka District, uplands 1480 m., on trees in *Brachystegia mimosaefolia* scrub woodland, *C. G. Trapnell*, at Kew.

S. RHODESIA: Matapos District, 1610 m., *Frederick Eyles 1023 p. p. min.*, at Kew.

102. USNEA TRICHODEOIDES Vainio, Ann. Acad. Sci. Fenn. A 6^7:8. 1915; emend. Motyka, Lich. Gen. Usnea Stud. Monog. 421. 1937.

Usnea longissima f. *Ebersteinii* Stein, Jahresber. Schles. Ges. Vaterl. Cult. 66:133. 1888.

Type: Cape of Good Hope, com. *Persoon*, in herb. Acharius at Helsinki. Motyka based his description on Tanganyika, Usambara, *C. Holst 2642*. Type of *Usnea longissima* f. *Ebersteinii* Stein, from Tanganyika, Kilimanjaro, Rabai Ndaru in scattered forests in steppes, *H. Meyer*.

Thallus up to 40 cm. long, pendent, very flaccid, ecorticate, axis colonial buff to white, corticate, ramuli deep olive buff; dichotomous just above the holdfast, then rarely dichotomous throughout, the branches soon parallel, straight or slightly flexuous; axis 0.4–0.6 mm. in diameter, slightly thinner at each dichotomy to the capillaceous summits, terete to slightly flattened and occasionally very faintly longitudinally rugose; cortex soon flaking off, leaving a farinose, subsorediose surface on most of the branches except the smallest, sometimes with a few minute spinules (isidia?); ramuli close, somewhat variable in length, 3–10 (–15) mm. long, corticate, terete, smooth, tips acuminate, the longer dichotomous near the tips.

Apothecia (absent from most of our material) subterminal on stouter ramuli, 3–8 mm. in diameter; exciple slightly lacunose to smooth; marginal cilia few, about 10 mm. long, often broken off; disc nearly plane, flesh color, lightly but distinctly pruinose.

The material referred here is rather variable. It differs from *U. arguta* Motyka in having axes more slender (0.4–0.6 mm. instead of 1 mm.), straight rather than tortuous, shorter, smooth ramuli 3–15 mm. long (instead of 10–30 mm.) with

irregularly disposed small sorediose tubercles; axis with pale yellow strands instead of subfuscous axes from strands of fuscous hyphae.

SUDAN: Onyiro, Issore, 1770 m., 3° 50′ N., 32° 50′ E., *T. F. Chipp 57*, a fragment, at Kew.

KENYA: Mt. Elgon, 2790 m., *E. J. Lugard & Mrs. Cyril Lugard 470*, at Kew; Loita plains 40 and 60 miles southeast of Narok, 1610–2250 m., *Anita G. Curtis 669b, 743c*, in Dodge herb. det. Motyka, and at Farlow Herb.; Lake Ngunga, 1775 m., on trees, *G. M. Allen 1788* in Howe herb. sub *U. longissima*, at Farlow Herb.

UGANDA: Ruizi River, 1550 m., *T. Jarrett 402*; Bugishu, Butandiga, 2410 m., *A. S. Thomas 484*; Kigezi, Kasatoro, Kabale River, 2250 m., *I. R. Dale L43*; Mt. Elgon, 1290 m., *W. Small 216*; without locality *H. Fyffe 167*; all at Kew.

CONGO: Mt. Kahusi, ca. 2700 m., on *Arundinaria alpina*, *F. L. Hendrickx 4302*, in E. African Herb.

TANGANYIKA: Bukoba, Kabobwa, Mingito Forest Reserve, 1550 m., *G. Watkins 492* (Forest Dept. Herb. 3231, native name: *machankima*), sheets at Kew and in E. African Herb.; Maruessa between Duruma and Taita, *Hildebrandt* com. C. Rensch ex herb. Sbarbaro, at Farlow Herb.

ZANZIBAR ISLAND: without locality, *J. H. Vaughan 1359*, at Kew.

MOZAMBIQUE: Inhambane, on *Copaifera*, without collector, at Kew.

SOUTH AFRICA: Gnove [?], *Drège*, com. Laurer ex herb. Sbarbaro; Uitenhage District, in forest, *Ecklon*, ex herb. W. Sonder in Tuckerman herb.; both at Farlow Herb.

STUDIES IN THE CAPPARIDACEAE. III

Evolution and Phylogeny of the Western North American Cleomoideae*

HUGH H. ILTIS**

One of the best ways to visualize evolution is to arrange related forms in the order of their complexity. With fairly large and complete series, it is possible to show graphically the homology of unlike extremes by observing the intermediates. Use of the so-called reduction series (Woodson, 1935) such as the modifications described by Bower (1923) and by Zohary (1948) is open to severe criticism, since they are composed of contemporary types not in direct line of descent (Lam, 1951). Nevertheless, they help to elucidate such problems as relationships between species and species groups, direction of evolution, and morphology of derived structures, particularly in cases where paleobotanical and cytogenetical evidence is lacking.

The Capparidaceae, as well as the whole of Rhoeadales, provides a wealth of series illustrating many evolutionary problems (Camp, 1950). Four western North American genera of the subfamily Cleomoideae, namely *Cleome* sect. PERITOMA, *Cleomella, Wislizenia,* and *Oxystylis,* constitute one of the most clear-cut "reduction series," and their taxonomy, morphology, geographical distribution, intra- and inter-generic relationships, and intra-specific variations are discussed in this paper. Based on the above, an attempted evolutionary interpretation is correlated with the geologic history of North America and is discussed in the light of the probable great importance of desert evolution in this group and the angiosperms generally.[1]

I. Taxonomy

The Capparidaceae is a member of the Order Rhoeadales, with the Cruciferae its closest, most specialized relative. The 40 genera and 700 species of Capparidaceae, occurring mainly in the tropics of both hemispheres, are customarily separated into two major subfamilies: Capparidoideae and Cleomoideae. The Capparidoideae includes forms, mainly shrubby or arborescent, with fleshy, indehiscent fruits. Its largest genus is *Capparis,* the pickled flower buds of the Old World *C. spinosa* furnishing the capers of commerce, a seasoning for food. The Cleo-

[1] I should like to express my thanks to the Institute of Science and Technology, College of Arts and Sciences, University of Arkansas, and to the Department of Botany, University of Wisconsin, both of which gave me support during the course of this study; also to the Society of Sigma Xi, for a grant-in-aid. Many friends have given me much encouragement and helpful criticism: Drs. G. T. Johnson, R. C. Rollins, L. H. Shinners, and particularly Drs. Royal Shanks and A. J. Sharp, of the University of Tennessee; and Drs. George B. Van Schaack, R. M. Tryon, and R. E. Woodson, of the Missouri Botanical Garden, St. Louis, where a minor portion of the present paper was used as part of a master's thesis (Iltis, 1950). My wife, Grace Iltis, has provided encouragement throughout this study, and her interest and counsel are here gratefully acknowledged.

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moideae are mostly herbaceous and annual, rarely shrubby. The fruits are usually dehiscent, unilocular capsules (siliques) with two generally deciduous valves attached to a persistent replum (placenta). This subfamily includes the small North American genus *Polanisia* and the world-wide genus *Cleome*, with about 180 taxa, 83 of which occur in the Western Hemisphere (Iltis, 1952, 1955b). Of these, some are known for their showy flowers, such as *C. houtteana* Schlecht. ("*C. spinosa*" hort.), the Spider Flower, and *C. serrulata* Pursh, the Rocky Mountain Bee Plant.

SYNOPSIS OF THE TAXA CONSIDERED IN THIS STUDY

(Probable relationships diagrammed in fig. 16)

A. *Cleome*[2] sect. PERITOMA (DC.) Baill.
1. *C. lutea* Hook. (including var. *jonesii* Macbr.)—Yellow Bee Plant, Stinking Mustard
2. *C. isomeris* Greene (*Isomeris arborea* Nutt.)—Burro Fat, Bladder Bush
3. *C. platycarpa* Torr.
4. *C. serrulata* Pursh—Rocky Mountain Bee Plant
5. *C. multicaulis* Sessé & Moc. ex DC. (*C. sonorae* Gray)
6. *C. sparsifolia* Wats.

B. *Cleomella* DC.[3]
1. *C. angustifolia* Torr.
2. *C. longipes* Torr.
3. *C. perennis* Iltis
4. *C. mexicana* Sessé & Moc. ex DC.
5. *C. palmerana* Jones (a complex including *C. cornutae* Rydb., *C. montroseae* Payson, *C. nana* Eastw.)
6. *C. hillmanii* A. Nels. (including *C. macbrideana* Payson)
7. *C. obtusifolia* Torr. & Frem., *sensu lato*
8. *C. plocasperma* Torr. & Frem. (*sensu* Abrams, 1944)
9. *C. parviflora* Gray (including *C. alata* Eastw., *C. gracilis* Brandg.)
10. *C. brevipes* Wats.

C. *Wislizenia* Engelm.[4]
1. *W. refracta* Engelm. (including all nine species described by Greene (1906) and others.)—Jackass Clover, Stinkweed, Spectacle Pod

D. *Oxystylis* Torr. & Frem.
1. *O. lutea* Torr. & Frem.

II. General Morphology

The eighteen species enumerated above share such a large number of vegetative and floral characters that it is sometimes difficult to distinguish between flowering plants of two genera. All species are small or medium-sized plants (figs. 4–6), annual (except *Cleome isomeris*, *Cleomella perennis*, *C. mexicana*, and, rarely, forms of *Wislizenia*), though not always ephemeral, and are essentially glabrous (except *Cleome platycarpa* and *Cleomella obtusifolia*). The leaves are compound, with 3 (in *Cleome lutea* 5) entire leaflets less than 6 cm. long, succulent and thick, more or less conduplicate and often glaucous, these usually tipped by a thick, usually varnished mucro or by a slender scarious hair.

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[2] A comprehensive monograph of *Cleome* in the New World, written as a doctor's thesis, is awaiting publication (Iltis, 1952).

[3] In the only published revision of *Cleomella* (Payson, 1922), the species concept is too narrow. Crum's (1929) unpublished thesis was useful in my studies, which cover all species except *C. angustifolia* and the *C. palmerana* complex.

[4] The many variants here are best divided into the eastern *W. r.* var. *refracta*, the northern *W. r.* var. *melilotoides* (Greene) Johnston, and the southwestern *W. r.* var. *palmeri* (Gray) Johnston (cf. Johnston, 1924). Kuntze (1903) considered *Wislizenia* a section of *Oxystylis*.

One significant peculiarity of all but two taxa *(Cleome isomeris, C. platycarpa)* is the possession of microscopic whitish, filiform or laciniate, scarious stipules[5] on either side of the petiole base or, in ebracteate flowers, at the base of the pedicel (figs. 7–8). These stipules are inconspicuous, and commonly break off in old stems. Their frequency emphasizes close relationship, since in other Cleomoideae such structures are found only in a few species of *Cleome* and rarely in *Polanisia.* Morphologically, they seem to be homologous to the minute, gland-like stipules of the Resedaceae, concerning whose nature there have been so many divergent views (Bolle, 1936). In the opinion of Hennig (1929) they are probably reduced stipules. The presence of these anomalous structures is additional evidence of relationship between the two families.

The tetramerous, usually weakly zygomorphic flowers, borne in racemes (figs. 4, 5, 8) are characterized by frequent occurrence of persistent or tardily deciduous, synsepalous calyces, by sessile or subsessile petals, and tightly coiling mature, dry anthers. The flowers, in general, are larger in *Cleome* than in the other genera. The petals are yellow in all species except the purple or pink *Cleome serrulata* and *C. multicaulis,* and have a convolute (closed) aestivation. A structure that varies considerably is the more or less eccentric nectariferous disk between corolla and androecium which is highly complex in some species. All species seem to be insect-pollinated (Pellett, 1930; Jepson, 1936).

The truncate or pointed stigma (in *Cleome multicaulis,* somewhat capitate) and the slender, indurate style (fig. 3) point to the general specialization of this group, since I consider sessile, capitate stigmas as primitive. This view agrees with that of Zohary (1948) regarding the Cruciferae.

The seeds vary in size and ornamentation, but in structure are basically uniform, being reniform, globular to ovoid, somewhat flattened and characterized by a deep invagination, with the embryo, as in all Cleomoideae, curved and notorhizous (conduplicate). The two parallel ends, or "claws," may remain open (as in *Polanisia* and most Old World species of *Cleome*), or they may be fused exteriorly by a thin membrane or the thick testa, as in nearly all New World Cleomoideae. In the four genera treated here the two "claws" are fused internally as well, save at the very tip. The lack of a cavity inside the seed is also a specialized condition, for in primitive tropical species, e.g., *Cleome parviflora* or *C. spinosa,* the internal sinus between the claws is large. All species inhabit semi-arid or arid regions of western North America (figs. 9, 12), such as deserts, semi-deserts, sagebrush *(Artemisia)* associations, alkali flats, and grasslands, occurring often in "badlands" and in gravelly or sandy, dried-up river beds and shores. Most species occur in alkaline and saline soils, with some definitely halophytic.

In summary, the uniformity of most vegetative and floral structures justifies the assumption of this as a coherent group of closely related taxa.

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[5] The "stipular" thorns or spines of *Cleome* and *Capparis* are apparently epidermal outgrowths, not foliar in nature.

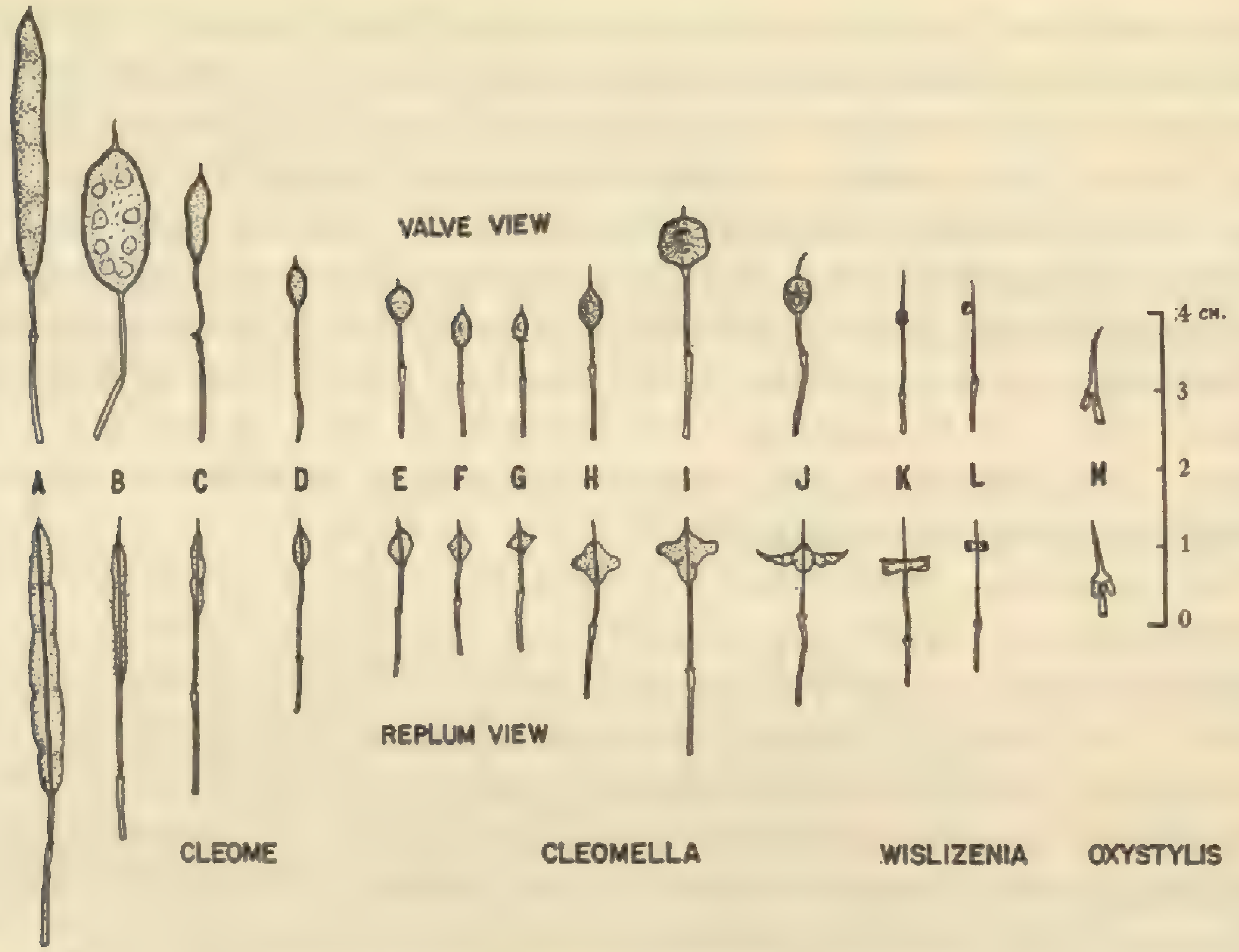

Fig. 1. Fruit reduction series of the North American Cleomoideae:
A, *Cleome lutea*; B, *Cleome platycarpa*; C, *Cleome multicaulis*; D, *Cleome siliculifera* (Brazil); E, F, *Cleomella palmerana*; G, *Cleomella plocasperma*; H, *Cleomella obtusifolia*; I, *Cleomella hillmanii*; J, *Cleomella obtusifolia* var. *taurocranos*; K, *Wislizenia refracta* var. *palmeri*; L, *Wislizenia refracta* var. *refracta*; M, *Oxystylis lutea*.

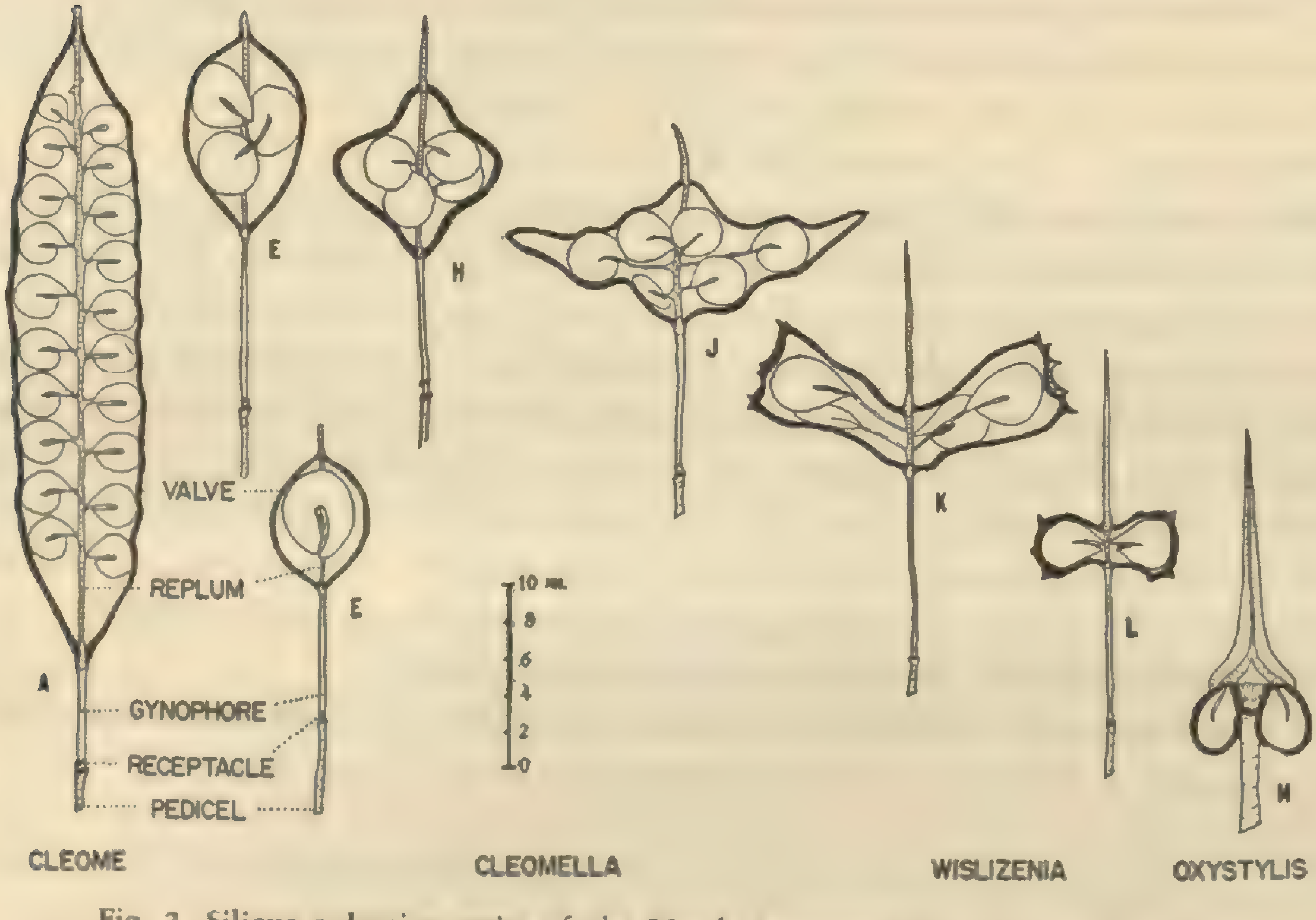

Fig. 2. Silique reduction series of the North American Cleomoideae. Letters correspond to those of fig. 1.

III. Morphological Basis for an Assumed Generic Phylogeny

The fruits, racemes, and stipules of the four genera discussed may be arranged in phylogenetic series, in which we can follow each from *Cleome,* through *Cleomella* and *Wislizenia,* to its greatest modification in *Oxystylis.*[6]

1. *Modification of the Fruit.*—

The changes are most striking in the fruit. Indeed, this "reduction series" suggested the current study.[7] The basic fruit type of the Cleomoideae is the silique, but of the four genera only *Cleome* has siliques, a fruit type that is considered primitive in this family as well as in the whole order (Zohary, 1948).

All species of *Cleome* sect. PERITOMA have dehiscent siliques formed by two valves attached to an elongated replum on which the 8 to 30 or more seeds grow. When the fruits are ripe the valves fall off, permitting the seeds to fall free while the replum remains attached to the plant (fig. 10A). Interjected between silique and receptacle is the gynophore (fig. 2), a slender stalk 5–40 mm. long. Both gynophore and pedicel elongate somewhat after flowering. Some Cruciferae have similar siliques except that a false septum is drawn across the replum making the pod two-chambered.

The siliques of two *Cleome* species may help us to understand the evolution of the *Cleomella* silicle. (1) *Cleome lutea,* primitive as the only species with five leaflets, has fruits that vary from only 8 mm. long in depauperate plants of var. *lutea* to 80 mm. in var. *jonesii.* In the short fruits and general habit, var. *lutea* at times strongly resembles *Cleomella angustifolia* and *C. longipes.* (2) *Cleome platycarpa,* primitive in its floral structure but otherwise specialized, has siliques anomalous in their strong compression (fig. 1B), with flat valves attached to a broadly oval replum tipped by a long style. A roundish replum, rare in *Cleome,* is usual in *Cleomella.* Hence, in replum shape *Cleome platycarpa* is intermediate between *Cleome* and *Cleomella.* Young plants of *Cleome platycarpa* closely resemble those of *Cleome hillmanii,* a similarity probably due to convergent or parallel evolution.

Cleomella fruits (fig. 4) are *silicles,* short siliques not much longer than wide. The repla are oval to round (fig. 1 E–J, top row), similar to those of *Cleome,* but wider and smaller. Viewing the fruits from the side (fig. 1 E–J, bottom row), however, we find a variety of shapes caused by lateral expansion of the valves, ranging from hemispheres to obtuse or acute cones or horns (fig. 1J). Some *Cleomella* species may have fruits very similar to the unrelated South American *Cleome siliculifera* Eichl. (fig. 1D) or abnormally small-fruited *C. lutea.* As in *Cleome,* the seeds fall free (fig. 10B).

The tendency of *Cleomella* valves to expand laterally correlates with: (1) the

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[6] Evidence for establishing the generic phylogeny of *Cleome* and *Cleomella* was derived mainly from the morphology of the primitive taxa in each genus. Nevertheless, the phylogeny within a genus, particularly in *Cleomella,* is worth noting since many trends from primitive to specialized species are homologous to and parallel those of the series *Cleome* → *Oxystylis.*

[7] I am grateful to my esteemed teacher, R. E. Woodson, Jr., who interpreted for me this sequence, thus introducing me to the concept of "reduction series" (Woodson, 1935).

obvious decrease in length of gynophore, pedicel, and fruit (½ to $\frac{1}{20}$ the length of *Cleome* siliques), particularly in the Great Basin species; and (2) the radical decrease in seed number (2–12 (–20) per silicle, cf. fig. 2). Here, while decrease in fruit *size* is accompanied by only a minor decrease in seed *size*, the seed *number* decreases markedly. By contrast, in other groups of *Cleome* with reduced siliques (West Indian "UNIFOLIOLATAE"; North African sect. THYLLACOPHORA Franch.), seed size is usually directly proportional to silique size, with the seed number essentially constant.

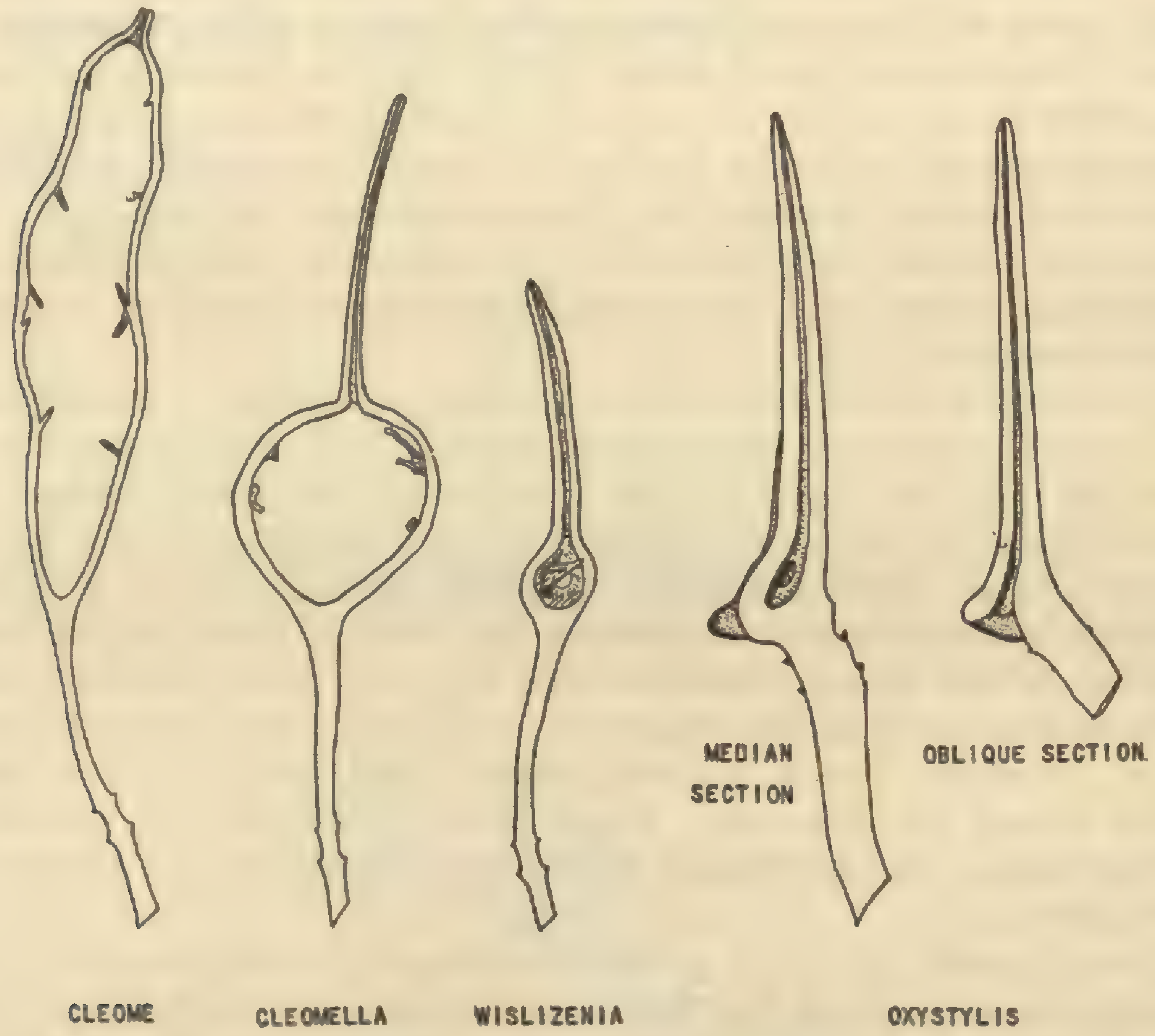

Fig. 3. Longitudinally sectioned fruits (i.e., gynophore-replum-style) after removal of valves and seeds.

Most variable in fruit shape is the Californian *Cleomella obtusifolia,* with obtusely conical valves in the typical form (fig. 1H) to narrowly conical ones in var. *taurocranos* (fig. 1, and 2J). In this most specialized fruit of *Cleomella* the valves are constricted at intervals. Due to this a single seed is often loosely imprisoned in the tip of each valve (fig. 10C), the valve and seed falling together at maturity—a rather insignificant and accidental matter were we to stop at this point! However, what we see is a feeble expression of an evolutionary tendency, hereafter called the "schizocarp tendency" which reaches great prominence in *Wislizenia* and *Oxystylis.*

The polymorphic, monotypic *Wislizenia* (fig. 5) differs sharply from *Cleomella* in fruit characters, the evolutionary trends already apparent in *Cleome* and *Cleomella* (figs. 1 and 2, K–L) being greatly increased. Thus, the repla, reduced to minute rings 1 mm. in diameter, tipped by long, slender styles (fig. 3), are borne on gynophores and pedicels, each only 5–12 mm. long. Because of the small replum, the shape of *Wislizenia* valves differs from those of *Cleomella*. Valves of *Cleomella* are hemispheric to narrowly conical, being *widest at the point of attachment to the large replum* and narrowest at the apex, while those of *Wislizenia* vary from obovoid or subspherical to obconical, being *narrowest near the point of attachment to the tiny replum* and widest near the middle in obovoid valves (fig. 1L) or at the apex in obconical ones (fig. 1K).

Thus, when the fruits mature, each valve permanently encloses its one or two seeds (fig. 10D). In *Wislizenia*, then, the fruit is really a schizocarp, with each of the two valve-seed units a mericarp. These could be thought of as nutlets, in which all but the seed tip (which may project partially through the basal pore of the valve) is enclosed by the ovary wall. We have here a continuation of the schizocarp tendency indicated in *Cleomella obtusifolia* var. *taurocranos*. Of the four ovules in each ovary, *usually only two mature into seeds*, although all may develop in the larger-fruited, primitive *W. r.* var. *palmeri*. This low seed number is a continuation of the trend already manifest in *Cleomella*.

The valves of var. *palmeri* are obconical and elaborately ornamented, while those of var. *melilotoides* are obovoidal and nearly smooth. However, the latter not only reach ultimate size and valve reduction, with but one seed in each valve, but the valves also resemble those of *Oxystylis*, the final genus in this sequence, in having small rounded mericarps with tightly held seeds. Furthermore, while both *Cleomella* and *Wislizenia* usually have divaricate valves, some races of the specialized northern *(melilotoides)* and eastern *(refracta)* varieties have valves which point unilaterally away from the plant, resembling those of *Oxystylis* (fig. 1L, top row).

Oxystylis lutea (fig. 6), endemic to the Death Valley region, shows to what high degree a generalized structure such as the Rhoeadalean silique may become modified. While its seeds and valves resemble those of *Wislizenia r. melilotoides*, the structure of style, replum, gynophore, and pedicel is radically different. The replum of *Wislizenia* (fig. 3) is a tiny ring. In *Oxystylis* (figs. 2 and 3), this ring undergoes great lateral and downward expansion and thickening, resulting in an "inverted V-shaped" tube with down-facing open ends (fig. 2M). From this modified "replum" a greatly thickened, elongated, spinescent style projects upward. The gynophore and pedicel, each about 1 mm. long, are also much stouter and shorter than in *Wislizenia* (fig. 8C, 8D).

Attached to the down-facing orifices of the replum are the two parallel and unilaterally protruding, obovoidal valves (figs. 1M, 6, 8D). Like those of *Wislizenia r. melilotoides*, they enclose their single seed tightly and permanently (fig. 10E), with but a minute pore at their attachment point. However, the thinner

and very smooth *Oxystylis* valves fit the seeds like seed-coats, which, functionally, they are.

We have traced the fruit modifications from *Cleome* through *Oxystylis*: (1) from large, elongate siliques, through round or laterally pointed silicles with divergent horizontal valves, to small schizocarps with nearly vertical, unilateral valves; (2) from fruits with many free-falling seeds to fruits where each valve and its single seed are inseparably joined and fall as one unit; (3) from fruits with short, slender styles and large elongated, hoop-shaped repla to those with long, spinescent, stout styles and small, tubular, "inverted V-shaped" repla; and finally (4) from elongate pedicels and gynophores to fruits in which these structures are short, stout, and nearly obsolete.

2. *Modification of Racemes and Bracts.*—

We may trace the modifications of racemes and bracts from primitiveness in *Cleome* to specialization in *Oxystylis*. The primitive Cleomoid inflorescence is a bracteate raceme. Through loss of bracts, ebracteate types have evolved independ-

Fig. 4. Open bracteate inflorescence of *Cleomella angustifolia*. Note long region of vegetative growth before flower production.

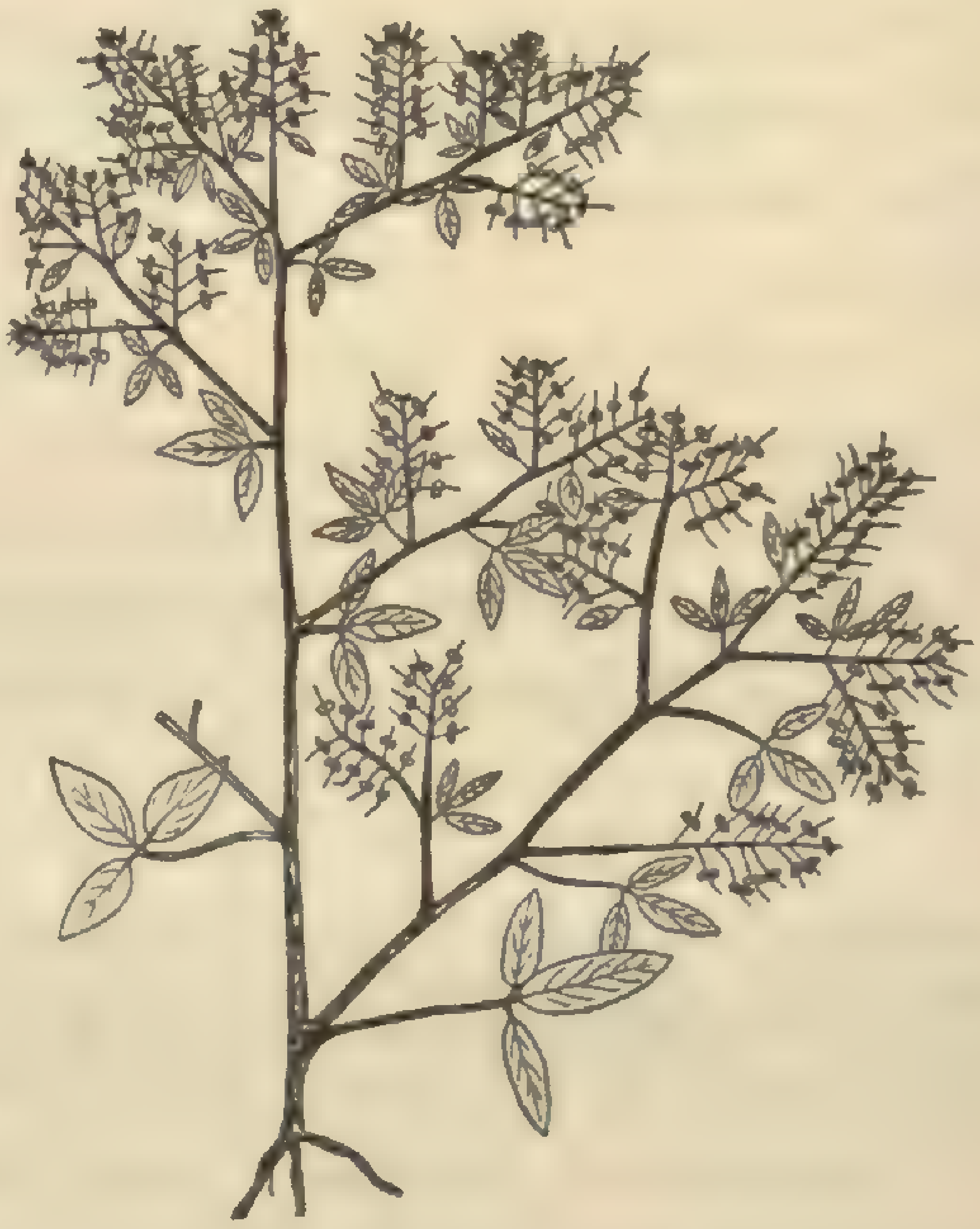

Fig. 5. Dense ebracteate inflorescences of *Wislizenia*.

ently at different times, with both bracteate and ebracteate racemes occurring in several genera (various groups of *Cleome* and in *Podandrogyne*). The ebracteate type generally characterizes specialized taxa.

Racemes are bracteate in *Cleome* sect. PERITOMA. One species *(C. multicaulis)* has 3-foliolate leaves not specially differentiated into bracts and of the same size and shape whether subtending flowers or not. In the other species of PERITOMA, however, all but the lowest bracts are 1-foliolate and easily distinguished from the multifoliolate cauline leaves.

Because racemes tend to be densely flowered at the apices and young bracts are very small, inflorescences may at first appear to be ebracteate. However, in time the bracts become foliaceous and after flowering the raceme axis elongates greatly, spacing bracts as well as the pedicels, so that the lower, older portions of a raceme are open and clearly bracteate (fig. 8A). Of the many flowers in each raceme, most are deciduous, only a few ovaries remaining to mature into siliques at well-spaced, cyclic intervals. Most older bracts therefore subtend only pedicellar scars.

Since *Cleome* racemes are indeterminate inflorescences, they continue apical growth for months, becoming quite long, over 6 dm. in some species. The individual racemes are clearly separate.

Racemes and bracts in *Cleomella*, particularly in the primitive *C. longipes* and *C. angustifolia* (figs. 4 and 8B) are much like those in *Cleome*. In some specialized species 3-foliolate bracts, which look like cauline leaves, occur throughout (*C. brevipes, C. obtusifolia, C. mexicana;* cf. Iltis, 1956). In other species a *tendency toward bract reduction* is quite evident, and racemes are often apically ebracteate.

Plants of *Cleomella* tend to be smaller and more branched than those of *Cleome*. Their racemes, though separate, are more clustered and usually appear after less vegetative growth. Fruiting racemes are denser, for many more flowers mature into silicles.

In *Wislizenia* (figs. 5 and 8C), racemes are *always ebracteate*, sometimes resembling nearly bractless extremes of certain *Cleomella* species *(C. longipes)*. Some forms of *W. r. refracta* or *W. r. melilotoides* have profusely branched stems, each branch tipped by a raceme 1–2 cm. long (fig. 5). From this specialized type we can go all the way to the primitive var. *palmeri* where little-branched stems bear a few racemes 10–20 cm. long.

Mature racemes of *Wislizenia* are very crowded (fig. 8C), because up to 95 per cent of the flowers develop into fruits, while at the same time the raceme axes elongate only slightly after flowering. Though these inflorescenses are structurally racemes and therefore indeterminate, they are determinate in that they grow often less than 1 or 2 cm. in *W. r. refracta* and *W. r. melilotoides,* before growth is curtailed.

If a lateral branch system of *Wislizenia* (lower right, fig. 5), with its many short inflorescences, were telescoped into a head-like "bur" about $\frac{1}{10}$ its original size, one of those peculiarly congested, axillary, compound inflorescences characteristic of *Oxystylis lutea* (fig. 6) would be obtained. Each of these raceme clusters

is borne singly in the axil of a well-developed leaf, and each leaf, *even the very first,* subtends such a cluster. The center of each cluster is composed of one to several stout, short, straight or branched central axes from which diverge 5–15 stubby side branches, densely covered with flowers or fruits. Each side branch, rarely over 1 cm. long, represents a raceme and may bear as many as 40 flowers though not all develop into fruit (fig. 8D,E). That this congested multitude of racemes is homologous to a branch system of *Wislizenia* is further borne out by the occasional occurrence of a large, normal leaf on the central axis at the base of one of the side branches (fig. 6, bottom right hand "bur"). Such leaves correspond to those usually found in *Wislizenia* at the base of each raceme.

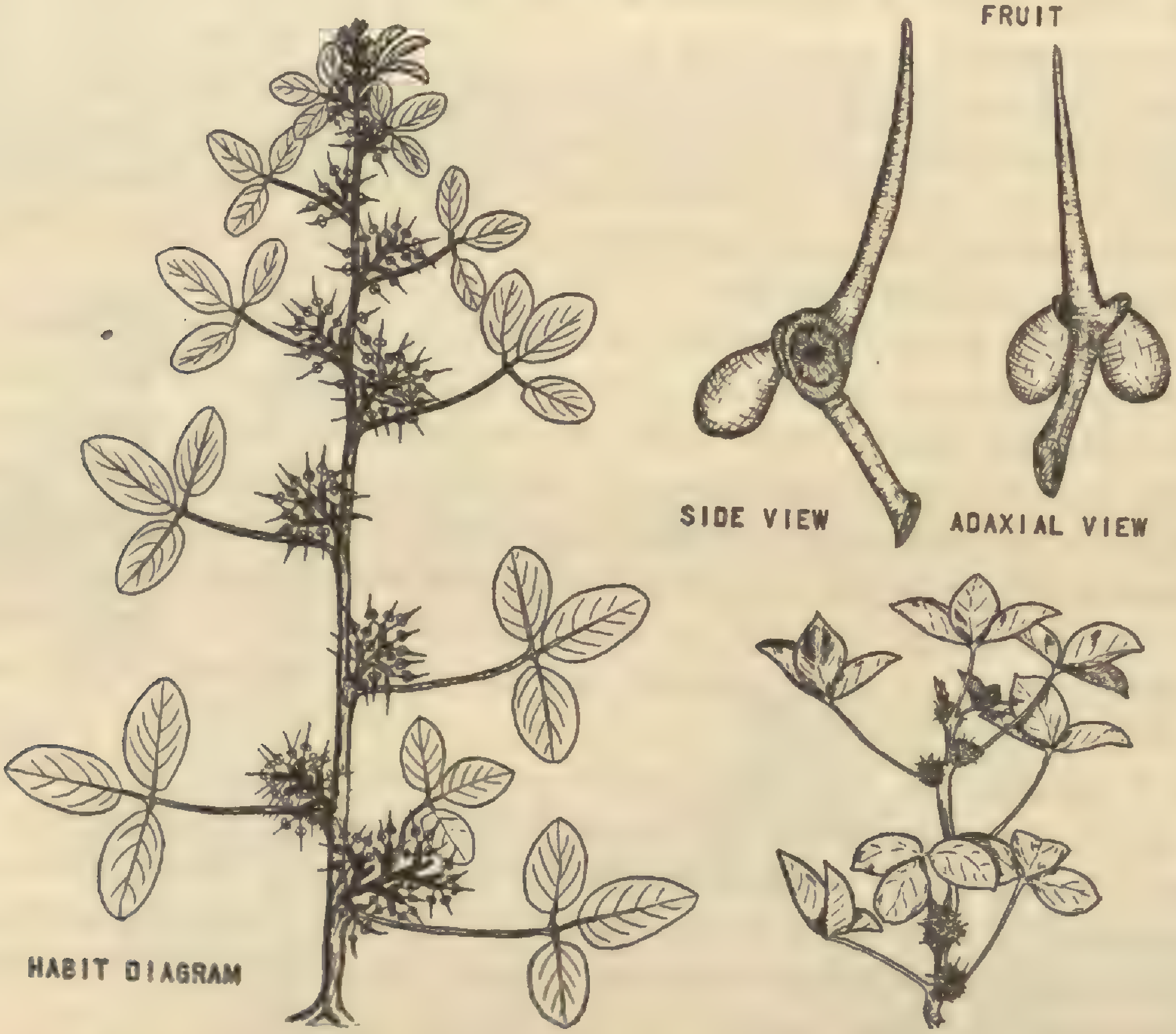

Fig. 6. Highly congested ebracteate inflorescence clusters of *Oxystylis.* Plant on right, with mature fruits; plant on left, very young and in flower (after Jaeger, 1941). Note exceedingly short region of vegetative growth before flower production.

The high development of four tendencies is responsible for the uniqueness of the *Oxystylis* inflorescence: (1) the essentially determinate, short growth of racemes; (2) the nearly total lack of post-floral elongation of raceme axes; (3) the almost complete elimination of non-floral sections of branch systems; and (4) the early initiation of flowering.

Thus again we have traced modification from primitiveness in *Cleome* to specialization in *Oxystylis.*

3. *Modifications of the Stipules.*—

We can trace modifications of stipules from *Cleome,* in which they are generally lacking, through *Cleomella* and *Wislizenia,* with progressively larger stipular bristles, to their eventual fusion into the flat complex structure in *Oxystylis.* Their occurrence in sixteen of the eighteen species under discussion emphasizes the phyletic coherence of the genera.

All species of *Cleome* sect. PERITOMA, except *C. isomeris* and *C. platycarpa,* have scarious, yellowish, bristle-like stipules, from 1–2 mm. long, occurring either

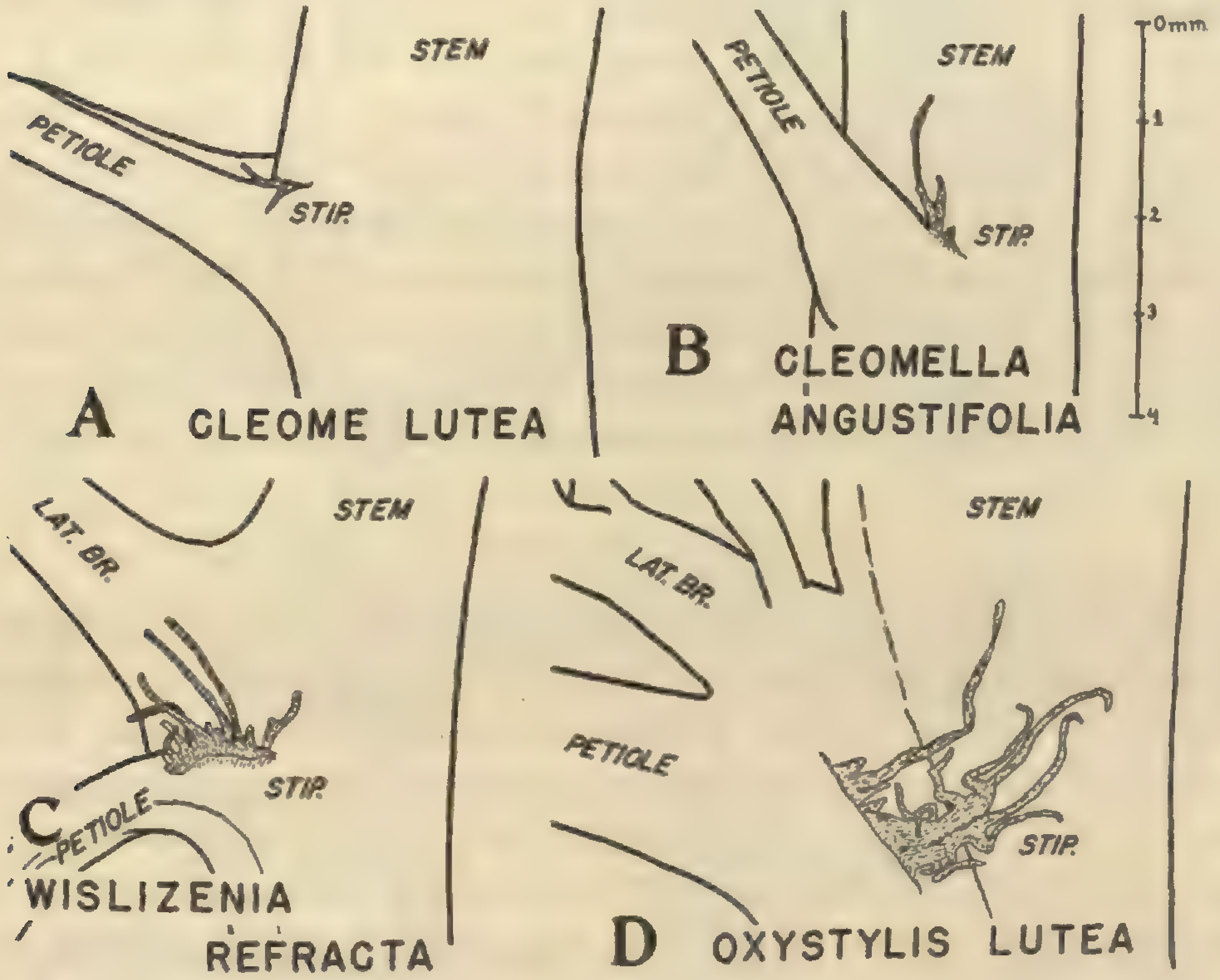

Fig. 7. Stipules of cauline leaves.

singly or in tufts of 2 or 3, on either side of the petiole base, of both cauline leaves and bracts.

Stipules of *Cleomella* generally resemble those of *Cleome,* but in some species tend to be longer (1–4 mm.), each tuft having 3–8 bristles. The largest are those of *C. obtusifolia,* noted by Watson (Gray, 1895), who erroneously cited the absence of stipules in all other species as a key character! Jepson (1936) made a similar error.

As in *Cleomella,* stipules in *Wislizenia*[8] occur in tufts each having up to 10 basally joined bristles of unequal length.

[8] These are the only stipules of the Cleomoideae regularly mentioned in the literature (Munz, 1935; Jepson, 1936; Pax and Hoffman, 1936).

In *Cleome* and *Cleomella* stipules are associated with the petiole bases of both the cauline leaves and flower-subtending bracts. *Wislizenia* and *Oxystylis* have cauline leaves with stipules but *no bracts!* Yet on the axis of the inflorescence, just beneath each pedicel base, well-developed stipules are found in the place where the petiole of the bract-blade would have originated were the inflorescence bracteate. This loss of blade and petiole but retention of stipules is an interesting case of unequal reduction of an organ. Furthermore, although the stipules on the inflorescence occur occasionally as two separate tufts, usually they are fused into a single prominent strip which makes them more conspicuous than in the two bracteate genera.

Oxystylis has the most specialized and the largest (2–4 mm. long) stipules of the four genera.[9] The other three genera have bristles which increase in number, length, and basal cohesion, from *Cleome* to *Wislizenia.* In *Oxystylis* these trends reach a climax in rather peculiar structures (fig. 7D): flat, very thin, and transparent central blades with 3–8 greatly contorted, flagellate, slender teeth. The stipules are most abundant and most easily observed on the stubby bractless racemes (fig. 8, D and E), but they also occur paired on the stems at the base of each cauline leaf (fig. 7D). They may be interpreted as groups of bristles such as occur on *Wislizenia,* joined for half their length to form the flat lamina, with the free ends forming the teeth.

4. *Other Trends.*—

In addition to the fruit, raceme, and stipule, there are less-prominent series which may be traced from *Cleome* to *Oxystylis.* Among these are reduction in size of flower and of seed, and minor changes in leaf shape. A summary of primitive versus advanced characteristics in the Cleomoideae has been published (Iltis, 1956).

Contrary to Bessey's dicta, the perennial habit of *Cleomella perennis, C. mexicana,* of some plants of *Wislizenia r. palmeri,* and of *Cleome isomeris* is definitely *not* primitive (Iltis, 1956). It can be interpreted as a specialized secondary character which in the Cleomoideae appears sporadically in several groups of grassland and desert species through convergent evolution.

IV. Interpretations of the Reductions and their Relations to Aridity

A study of the plant's environment considered in conjunction with its morphology may help to interpret the structural trends of the North American Cleomoideae from the primitive (*Cleome* sect. PERITOMA) to the most specialized genus (*Oxystylis*).

1. *Distributions in Relation to the Prevailing Climate.*—

The distribution of the four genera corresponds roughly to prevailing climatic patterns in western North America (figs. 9, 12). The comparatively unspecialized sect. PERITOMA of *Cleome* is widespread, occurring generally in more mesic regions,

[9] Despite the large size and peculiar structure of *Oxystylis* stipules, botanists have failed to notice them; some have even stated that they are lacking (Jepson, 1936).

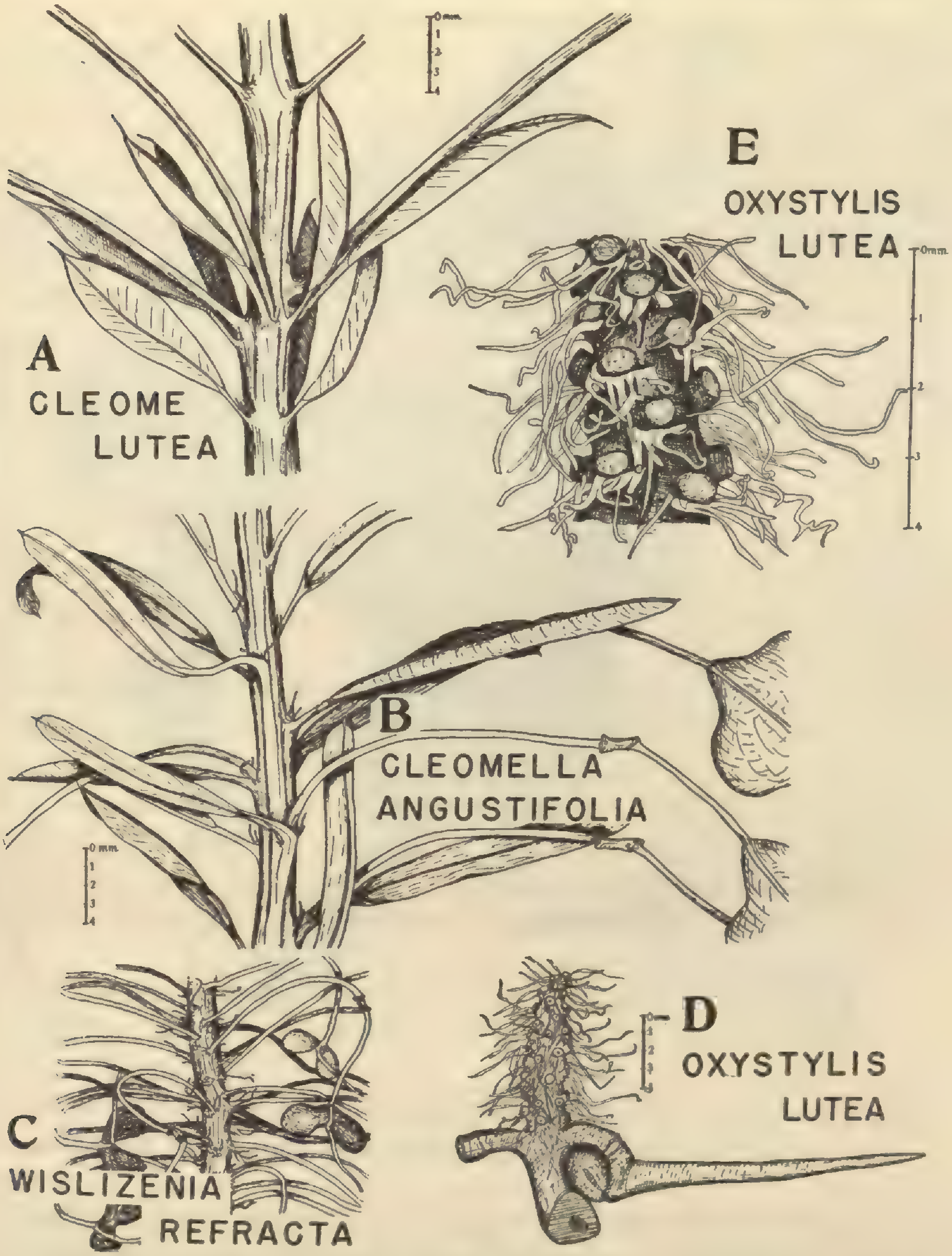

Fig. 8. Portions of inflorescences with stipules: A–D, drawn on same scale; E, enlarged portion of D. Note progressive condensation of raceme axis and increase in stipule size and length.

in less alkaline habitats, and at higher elevations. The more specialized genera, *Cleomella and Wislizenia,* occur in progressively more arid and alkaline habitats of lower elevations, and the most specialized genus, *Oxystylis,* is limited to the most arid and alkaline area of the continent, the Death Valley region of California and Nevada. This correlation between arid climate and morphological specialization[10]

[10] This applies not only to the generic level! The most specialized species within *Cleome* sect. PERITOMA *(sparsifolia)* and in *Cleomella (obtusifolia, parviflora, brevipes)* are likewise associated with some of the most alkaline, arid habitats of California and Nevada.

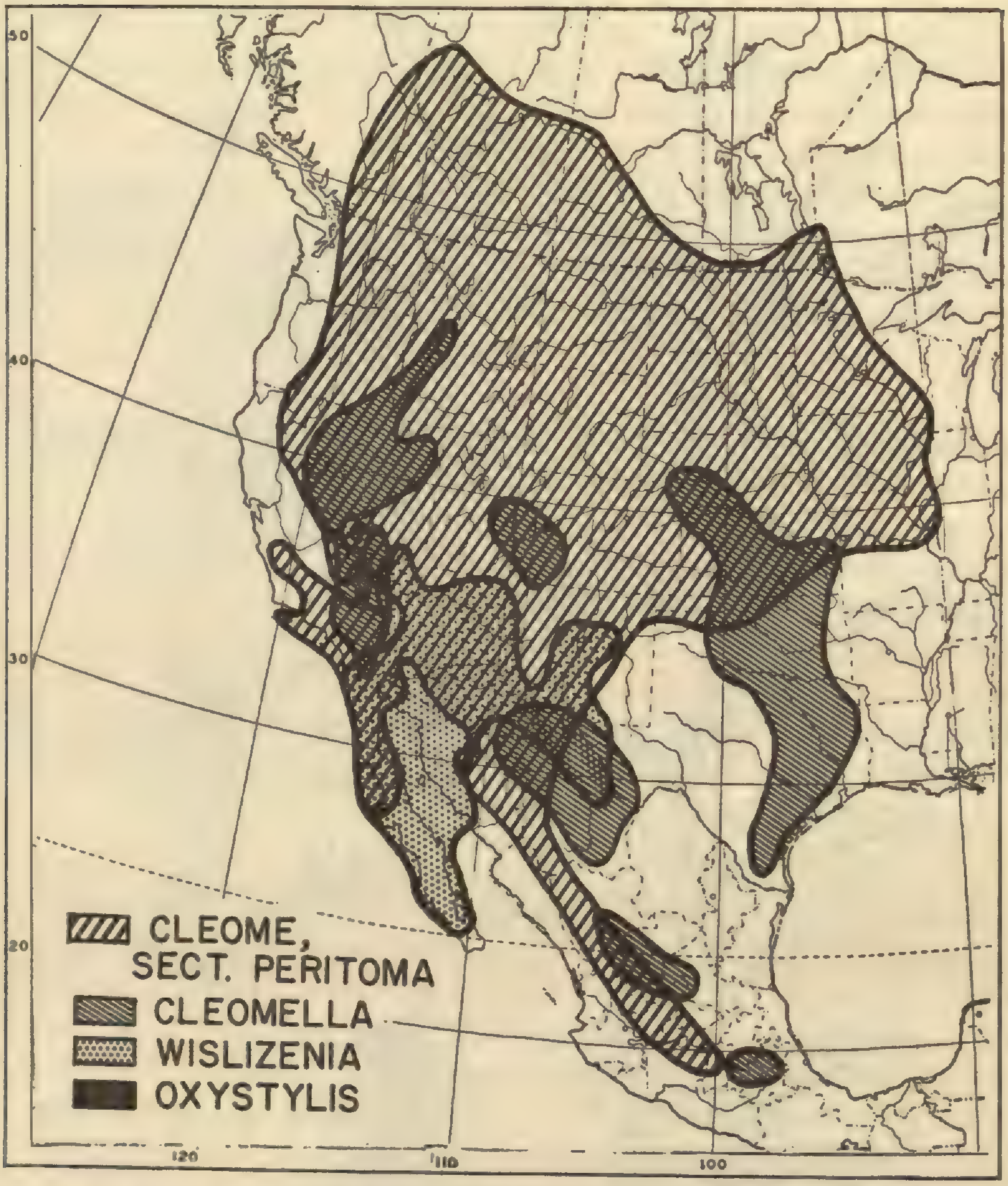

Fig. 9. Total distribution of the western North American genera of Cleomoideae.

implies *that these modifications are related in some way to desert environment*, and it is tempting to make the conventional assumption that they are "adaptations" and have "survival value".

2. *Climatic Notes, Especially on Death Valley and the Mojave Desert.*—

In nearly all environmental aspects, Death Valley is extreme (Thompson, 1929; Anon., 1954; Went, 1955). According to Munz (1935):

> The [mean?] temperature in the Mojave Desert is about 100° F., this prevailing between five and eight months out of the year. The extreme temperature of 134° F. at Greenland Ranch in Death Valley has been reported. Except in higher areas, the rainfall does not exceed five inches and often is under three inches. In Death Valley, which is 296 [282 according to Anon., 1954] feet below sea level, the lowest point in the United States, *two inches of rain is a maximum* [4.2 in 1941, the wettest year (Went, 1955)], *and a minimum of zero is of frequent occurrence.* The entire desert climate is one of unusually high summer temperature with resulting low humidity and high evaporation. [*italics* mine]

Coville (1893) states:

> The observations on the temperatures of Death Valley in 1891 for the hottest month of the year, July, show an average daily maximum of 116°, an average daily minimum of 87°, and a mean of 102° F. A maximum temperature of 122° occurred five times during the summer; these temperatures were taken under cover of a shelter constructed especially to eliminate the effect of radiation from the ground . . . In direct sunlight bodies that readily absorb heat must reach a temperature many degrees in excess of the recorded maximum.

According to Parish (1930) the record of 134° F., "when the mercury rose to the top of the tube", would have been exceeded in an instrument of greater range, and "such temperatures in the shade would indicate at least 150° F. in the sun". This temperature "is the highest natural-air temperature that has been recorded on the earth's surface by means of a tested, standard thermometer exposed in a standard ventilated instrument shelter" (Thompson, 1929).[11]

Soil temperatures must be even higher. MacDougal (1908) reports 148° F. in sandy soil surrounding roots of annuals at the Grand Canyon in Arizona. On a sunny summer day, soil temperatures in Death Valley must certainly greatly exceed 148° F.!

Precipitation varies from year to year, with the average annual rainfall (Went, 1955) 1.35 inches. Over a ten-year period (Thompson, 1929) the average monthly rainfall during November (0.20″), January (0.48″), and February (0.40″), accounted for 64 per cent of the yearly precipitation. During the rest of the year only rarely was there rain in excess of 0.10 inches per month, and in 64 out of 114 consecutive months there was no rain whatever. The rains that do come are usually in the form of hard, short showers.

3. *Some Prerequisites for Desert Survival.*—

With the environment so extreme and water supply so limited, a plant has to be specially adapted to survive; in short, it has "to make hay while it rains". The ability of seeds to take up water quickly after one of the rare showers, rapid germination, a short life cycle,[12] economy in growth and transpiration, and as rapid and large an output of seeds as the circumstances permit are all adaptations which seem essential to survival of desert annuals. The fruit and raceme modifications of the xerophytic Cleomoideae seem to have "developed in response to" two of the major demands of a desert environment: (1) the immediate and rapid germination of the seed during the rare times when water is available, and (2) the subsequent most rapid, most direct (or most economical) completion of the life cycle, i.e. production of seeds.

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[11] This world record was recently exceeded in Tripoli (136.4°, fide Anon., 1954).

[12] Dr. W. F. Blair (personal communication) tells me that in some Anura (e.g. *Scaphiopus*, the spadefoot toads) the length of the immature aquatic phase of the life cycle is generally correlated with aridity of native habitat. Toads in mesophytic areas reach the adult stage after many months of larval existence, while those in some parts of Texas complete metamorphosis in as short a time as twenty days.

4. *Xerophytic* vs. *Mesophytic Cleomoideae.*—

The differences between mesophytic and xerophytic Cleomoideae, of both Old and New World (cf. Iltis, 1956), may be generalized as follows: *Mesophytes,* as a rule, are 1–6 m. tall, have fewer, thinner, larger leaves with 3–13 narrowly elliptic, flat leaflets with long-attenuate apices, and produce flowers after considerable vegetative growth. Their fruits, commonly borne on long gynophores, are usually 5–10 cm. long (some 25 cm.!) and usually produce many fairly large seeds. The number of mature fruits per plant is frequently low. *Xerophytes* are rarely over 2 m., usually less than 1 m. tall, and have many small leaves. The 1–3 (–5, or rarely more) leaflets are often conduplicate, with obtuse to rounded or emarginate apices, those of the American species generally glaucous and fleshy. Some species flower and fruit when only 10 cm. tall; the Saharan *Cleome scaposa* may fruit when only 3 cm. tall (Kachkarov and Korovine, 1942) and *Cleomella brevipes* when only 1 cm. tall (Iltis, 1955b). The small fruits, often 0.5–3.0 cm. long, have many small seeds or few larger ones. The gynophore, often lacking or short, frequently reflexes over the pedicel. The number of mature fruits per plant tends to be very high. The above generalizations apply to most desert Cleomoideae, including such widely separated, unrelated groups as the western North American species, the West Indian "unifoliolate" species of *Cleome,* the Eurasian *Cleome* sect. THYLLACOPHORA Franch., etc. The occurrence of these characteristics in widely separated groups of desert plants is evidently due to convergent, adaptive evolution (cf. Briquet, 1914).

5. *Interpretations of the Reductions.*—

Most species of *Cleome* sect. PERITOMA and the primitive taxa of *Cleomella* (fig. 4) grow tall, have many leaves, greatly accrescent, bracteate inflorescences (fig. 8A) and large, many-seeded fruits, all structures requiring relatively large quantities of water and organic materials, and long growing seasons.

Most taxa of *Cleomella* (fig. 4) are smaller and often more branched than those of *Cleome* sect. PERITOMA. Inflorescences are shorter and frequently nearly ebracteate, and may appear earlier in the life cycle. The fruits are smaller, have fewer seeds, and mature more rapidly. The earlier appearance of flowers and the smaller fruit would result in shorter, or more economical life cycles.

Young plants of *Oxystylis* flower almost immediately after germination, with the earliest inflorescences in the axil of the first or second foliage leaf, an inch or less above ground (fig. 6). Compared with primitive species of *Cleome* or *Cleomella* (fig. 4), these plants do not waste time or water on much vegetative growth. The stems of *Oxystylis* are usually "unbranched"; its leaves are few. The inflorescences do not grow indefinitely as in Cleome, but after flowering they elongate at most a few millimeters, in sharp contrast to the striking postfloral elongation of the peduncle in most other Cleomoideae (fig. 8). Since the two-seeded fruits are very small, maturation is rapid. The lowest inflorescences of a plant 3 dm. tall may carry nearly mature fruits while the upper are still in flower.

To summarize: The series from *Cleome* sect. PERITOMA to *Oxystylis* shows

progressively less vegetative growth, increasingly early flower production, and more rapid maturation of fruits, the latter reflected in the reduction of fruit, pedicel and gynophore length, and in inflorescence elongation (cf. fig. 8). That these are adaptive modifications seems obvious. For example, if a 3 dm. tall *Cleome serrulata* should perish through environmental vicissitudes, it would probably leave no seeds to perpetuate the species, while even smaller plants of *Oxystylis* would have mature seeds. To quote Parish (1903):

> It is in these other areas that there is the greatest development of the protective adaptations which enable a plant most fully to utilize a scanty supply of water. The methods by which this is effected are three: by habits of growth; by provisions for storing supplies of water and food in times of plenty as reserves for times of need; and by contrivances for diminishing the loss of water through evaporation.
>
> The first of these methods is well exemplified by most of the xerophytic annuals. They spring up at once after light rains and put forth no more than a leaf or two before proceeding to the production of a flower and a fruit. If moisture now fails, reproduction is assured; should it continue to be supplied, branches are sent out and flowers and seed multiplied. Thus a plant when receiving only a little moisture may fulfill the cycle of existence and provide for the continuance of its species, without attaining an inch of stature; but under more favorable conditions it may attain dimensions of two or three feet.

Any change, therefore, that resulted in more economical vegetative growth and consequently more rapid production of flowers and seeds in some of the ancestral populations of *Cleome* sect. PERITOMA would have been advantageous either to their survival in a climate becoming progressively more arid or in the invasion of more arid regions. Those populations of *Cleome* that adapted to aridity by reducing the length of vegetative and fruit-producing periods appear to have given rise to *Cleomella,* whose ancestors, by the same process, produced *Wislizenia* and *Oxystylis.*

That reduced silique size probably evolved as a result of selection favoring shorter maturation periods and not for other reasons of economy, such as seed number reduction *per se,* is borne out in another way. In some species of *Cleomella,* and particularly in *Wislizenia* and *Oxystylis,* reduction in number of seeds from each flower is compensated for largely *by the much greater number of flowers that mature into fruits.* In fact, in some plants of *Wislizenia* nearly every flower produces fruits (fig. 8) which clothe the inflorescence so densely that the total number of seeds is greater than that of most plants of *Cleome.*

6. *Interpretation of the Schizocarp Tendency.—*

The evolution of the fruit reductions appears to have been indirectly associated with that of the schizocarp tendency in *Wislizenia* and *Oxystylis* where one or two seeds are permanently enclosed by the ovary wall (valve) (figs. 2, 10). This additional "seed coat" might help the plant to survive in deserts since it facilitates water uptake and retention, resulting in rapid seed germination, a well-known characteristic of desert plants. Thus, Bell (1953) reports a minimum germination time of nineteen days for a desert species and twenty-nine days for a mesophytic species of *Sanicula.* Seed germination in desert areas is necessarily closely tied up with rare, short and often violent showers.[13] At other times, according to Coville (1893),

[13] A discussion of seed germination in Death Valley and its relation to hard rains is given by Went (1955).

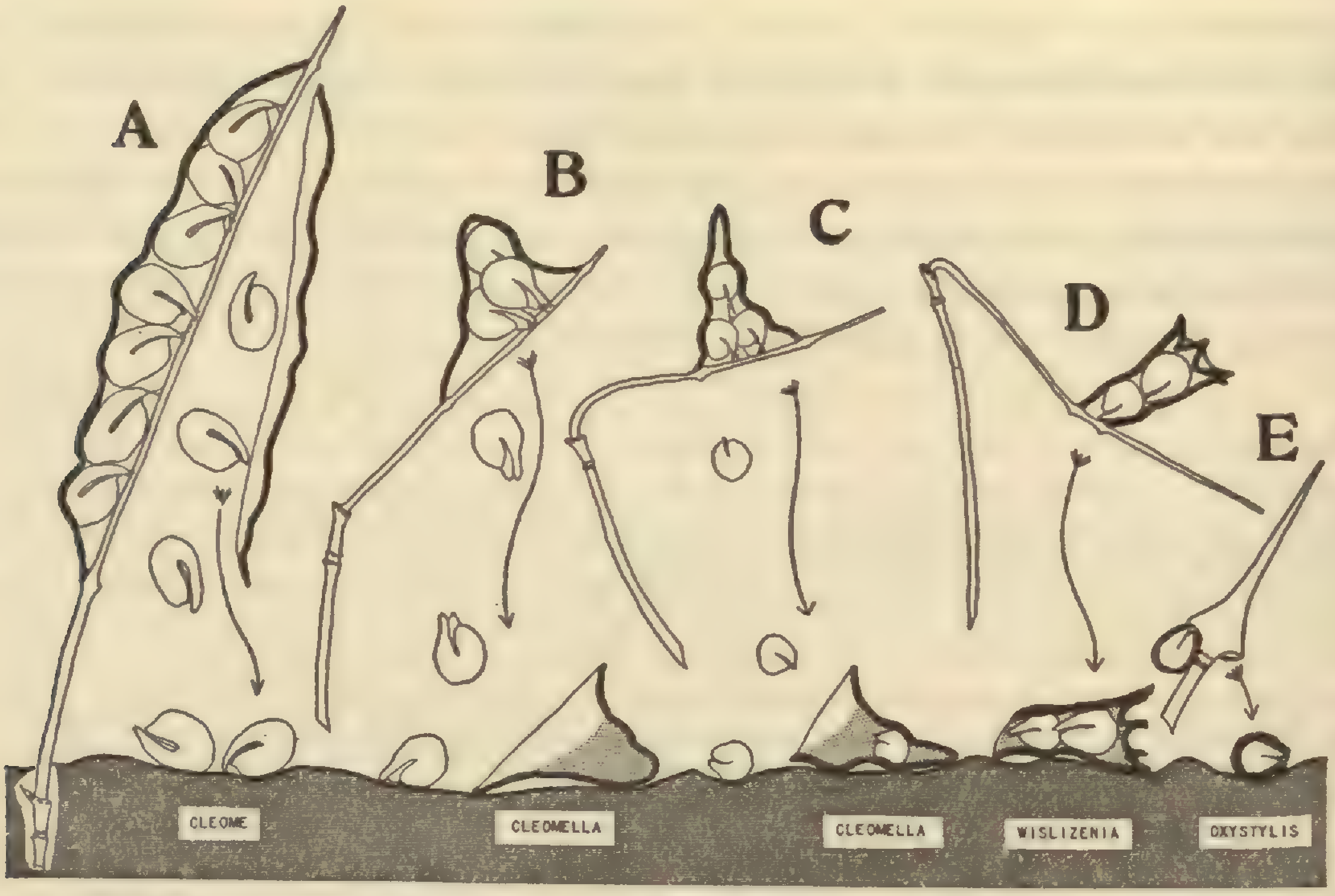

Fig. 10. Dehiscence of fruits and evolution of schizocarp tendency: A, *Cleome lutea* var. *lutea*; B, *Cleomella longipes*; C, *Cleomella obtusifolia* var. *taurocranos*; D, *Wislizenia refracta* var. *palmeri*; E, *Oxystylis lutea*.

water is practically non-existent since rain water quickly re-evaporates into a very dry atmosphere or is soaked up by a parched earth.

The ovary wall *appears* to function in two ways: (1) the soft tissues of the valve imbibe water and swell (fig. 10 C–E, black areas); (2) by capillarity, water enters through the mouth of the urceolate valve and fills the narrow spaces between valve and seed (fig. 10 C–E, black dots). Imbibition is probably of secondary importance in the development of the schizocarps since many Cleomoideae with free-falling seeds already have an outer testa with large blister-like cells which swell up when wet, thus retaining water for a time (e.g. *Cleome serrulata, C. lutea, Cleomella hillmanii* in North America; *Cleome arabica,* with very long, elongate hair cells, in the Sahara, etc.) Capillarity, however, appears to me to have been important in the schizocarp evolution. *We may postulate* that the tendency started in an ancestral *Cleomella* with fruits like those of *C. obtusifolia* var. *taurocranos* (fig. 10C), where one seed is loosely held by a constriction near the tip of the funnel-shaped valve. If such a valve falls off and becomes filled with water, the captive seed will have more water available for a longer period and hence a greater advantage over the free-falling seed in the availability of sufficient water to commence germination. Such a hypothetical race gave rise to *Wislizenia.* Here the valve is urceolate with a small basal opening, through which, on immersion, water enters, filling all spaces between the seeds and valve wall, the latter, in addition, becoming soft and spongy (fig. 10D). The one or two seeds are thus held in a water-filled "pitcher" which dries out slowly.

If this interpretation is correct, selective forces that furthered seed inclusion must have acted during the earliest germination phases of the life cycle. In contrast, selective forces that produced smaller fruit and foreshortened branches must have acted on later stages: vegetative growth, flowering, and fruit maturation. The two sets of adaptations, though produced by independent selection factors during different stages of the life cycle, are nevertheless historically interconnected since such schizocarpous fruits *could not have been produced* from *Cleome* siliques *unless preceded by drastic size reduction.* Not until fruits were as small and as laterally expanded as those of *Cleomella* was there any chance for the valves to curve around and imprison seeds. The fruit-size reduction from *Cleome* to *Cleomella* was then a prerequisite, a *preadaptation,* on which the schizocarp tendency of *Wislizenia* and *Oxystylis* was based.

7. *Differential Selection and the Critical Phase of the Life Cycle.—*
That fruit-maturation and pre-germination are the phases of the life cycle in these xerophytes during which selection pressures are greatest is suggested by the pronounced modification of fruits and racemes, and by the relative lack of modification in most other plant parts. In the Cleomoideae, desert survival is evidently not as closely tied up with the floral phases. The flowers, though specialized, are similar in all the genera, without any pronounced morphological trends as in the fruits or racemes, save decrease in size. There are sporadic instances of highly specialized floral structures, such as petal-nectaries *(Cleome sparsifolia)* and various specialized nectariferous disks *(Cleome* and *Cleomella)*. The thickish leaves, generally adapted to xerophytism and similar throughout, were changed only slightly, mainly from narrow and pointed to broad and emarginate leaflets.

These specific points agree with the generalizations of Stebbins (1949) that in sedentary plants "problems connected with reproduction and dispersal are far more important than those involved with maintenance". They also agree with many examples given by Stebbins of families (Gramineae, Cruciferae, etc.) in which flowers and leaves vary little, while fruits and inflorescences show a wealth of modifications.

Although the interpretations of the reductions are mostly conjectural, it would not be difficult in the Southwest to obtain data on the exact length of life cycle phases of each taxon, or to compare length of germination of artificially freed seeds of *Wislizenia* with that of seeds enclosed by valves.

8. *Orthoselection.—*
It is evident from the morphological series (fig. 1) that we are dealing with a kind of orthogenesis, *in the descriptive sense only,* which can be interpreted as the result of *orthoselection* (Huxley, 1943). This assumes that the same environmental forces that produced *Cleomella* continued on (though in increasing intensities) to produce *Wislizenia* and *Oxystylis,* and that if the same selective forces are operating on the same phyletic material, the same adaptive trends will continue.

Furthermore, a decreased gene pool resulting from high selection would seem to permit a group to evolve only within the limits of its available genetic potential.

9. *Classification of Modifications.*—

Timofeeff-Ressovsky (1940) classified morphological evolutionary trends into three groups:

(1) *Neutral,* which cannot be interpreted as *obvious* adaptations, there being no plausible relation between structure and environment. The larger stipules, or the tendency of the gynophore to deflex over the pedicel (*Wislizenia, Cleomella* spp.) are placed here though they might be consequential to certain other adaptive trends.

(2) *Adaptive,* where a plausible relationship between morphology and environment is evident. Most reductions studied here appear to belong to this group.

(3) *Harmonious modification.* In examining fruiting racemes of *Wislizenia* or *Oxystylis,* it is obvious that raceme foreshortening could not have taken place with large siliques but became possible after the fruits were reduced in size. Conversely, the many fruits could not have matured if the siliques were large because of spatial interference and problems of nutritive supply. Likewise, bract reduction is also prerequisite to foreshortening for there is not enough space for each *Oxystylis* flower to be supplied with a bract. Another "harmonious reduction" is the decrease in flower size with greater raceme density.

V. Geographic Distribution

1. *Geographical Distribution of the Genera and the Degree of Allopatry or Sympatry of the Species.*—

Cleome, with 180 taxa, is of almost world-wide tropical and sub-tropical distribution (fig. 11).[14] Of the 55 species and 25 subspecies indigenous in the Western Hemisphere, most are tropical. The six species of sect. PERITOMA are restricted to temperate, rarely subtropical, North America (figs. 12A, 13A) with their center of variation in eastern California and adjoining Nevada, where four species occur. All six species are to some extent sympatric, some with an overlap of ranges that is complete or nearly so.

The total range of *Cleomella,* (figs. 12B, 13B) though smaller than that of *Cleome* sect. PERITOMA, is similar in outline. The distribution of individual species is rather different. The five eastern and Mexican species are allopatric with sharply separated ranges. On the other hand, the Great Basin and Pacific slope area, with five species, contains many regions where two or three species occur together, but only one small region in south-central California, the center of variation of *Cleomella,* where four species are sympatric.

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[14] Distribution maps have been plotted from material of major U. S. herbaria (Iltis, 1955b), particularly the Missouri Botanical Garden Herbarium, and from sources that list individual localities, such as floristic works. Especially helpful was the unpublished thesis of Ethel Crum (1929), dealing with *Cleome isomeris, Cleomella* and *Wislizenia,* which cites many specimens. A microfilm copy of this work was kindly supplied to me by the University of California library through Miss Annetta Carter, to whom I should like to express my thanks. Generalized ranges, as given in floras, were found to be unreliable and were not used.

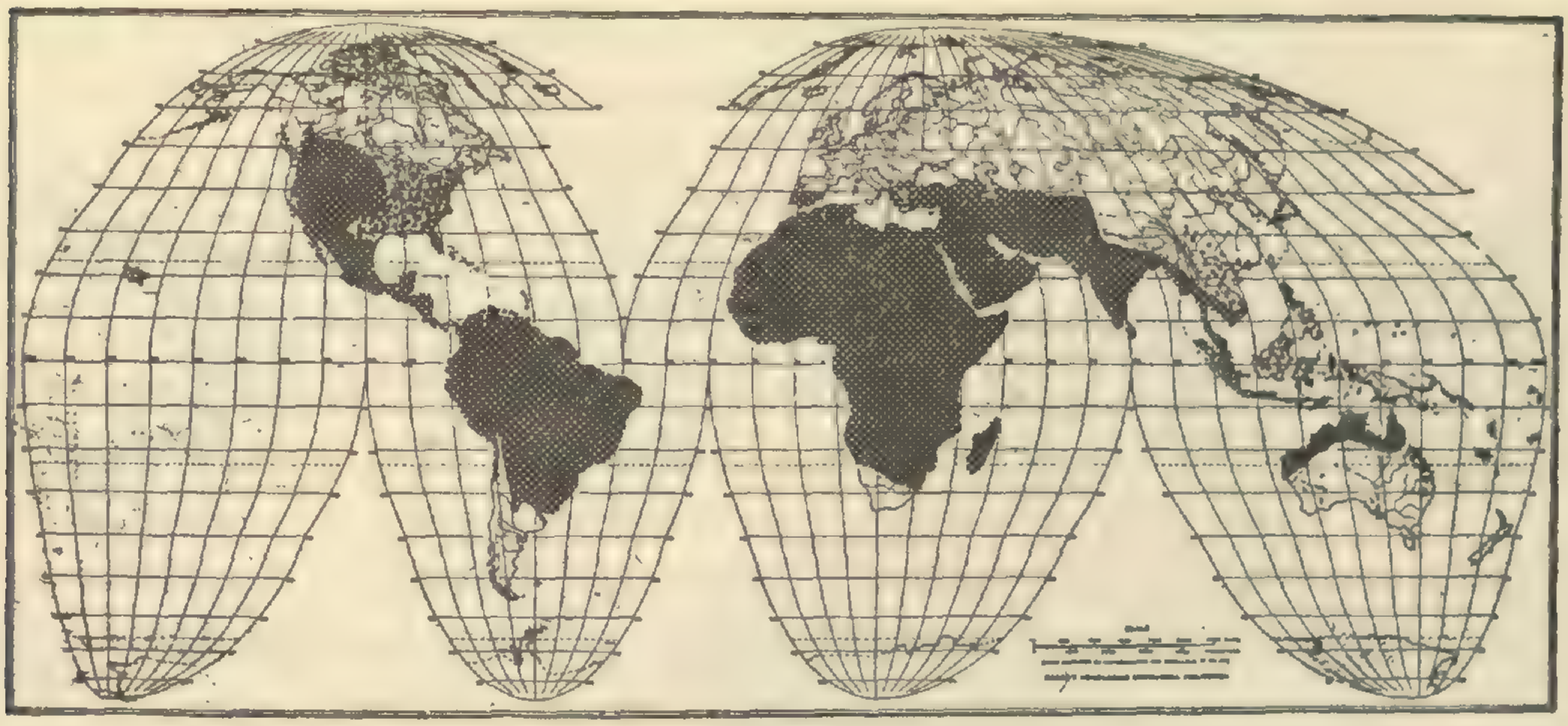

Fig. 11. Distribution of the genus *Cleome*: black with white dots, indigenous; black dots, adventive. Old World, about 90 taxa; New World, 79 taxa.

Wislizenia refracta occurs in the Southwest and adjoining Mexico. Its range is smaller than that of *Cleomella* and appears to be more or less continuous (figs. 12C, 13C), forming a horseshoe around the northern end of the Sierra Madre Occidental. *Wislizenia* spread as a weed into the San Joaquin Valley and other parts of California during historic times (Jepson, 1936), so that its natural range is smaller than the present-day, artificial range. Its morphologically diverse populations appear to be allopatric.

Oxystylis lutea is limited to deserts and washes of the Death Valley region in California and Nevada (fig. 12D, 13D). Most collections come from the Valley itself along the Amargosa "River" (marked on fig. 12D by a black line) where the species is reported to be abundant (Jaeger, 1941). A few specimens have been collected further north in Nevada. *Oxystylis* is a monomorphic taxon, and its populations are, therefore, allopatric.

The total generic ranges progressively decrease in size from the generalized *Cleome* sect. PERITOMA to the specialized *Oxystylis*. The regions in which the most widely distributed group (PERITOMA) occurs are generally rather mesic, while those of *Cleomella, Wislizenia* and *Oxystylis* are progressively more xeric, with *Oxystylis* thriving in the driest and hottest climate of the continent.

As to the geographic distribution within a genus, taxa in *Cleome* sect. PERITOMA are very highly sympatric; in *Cleomella* both sympatric and allopatric; and in the monotypic *Wislizenia* and *Oxystylis* the taxa (being the more or less differentiated populations) are allopatric.

2. *Geographic Distribution and Origin of Genera.*—

Taxa frequently evolve through geographic separation of one part of a population from another, and subsequent genetic and morphological differentiation of either or both of these isolated populations through different or unequal selection pressures (Mayr, 1942). That part of the original population which is isolated in

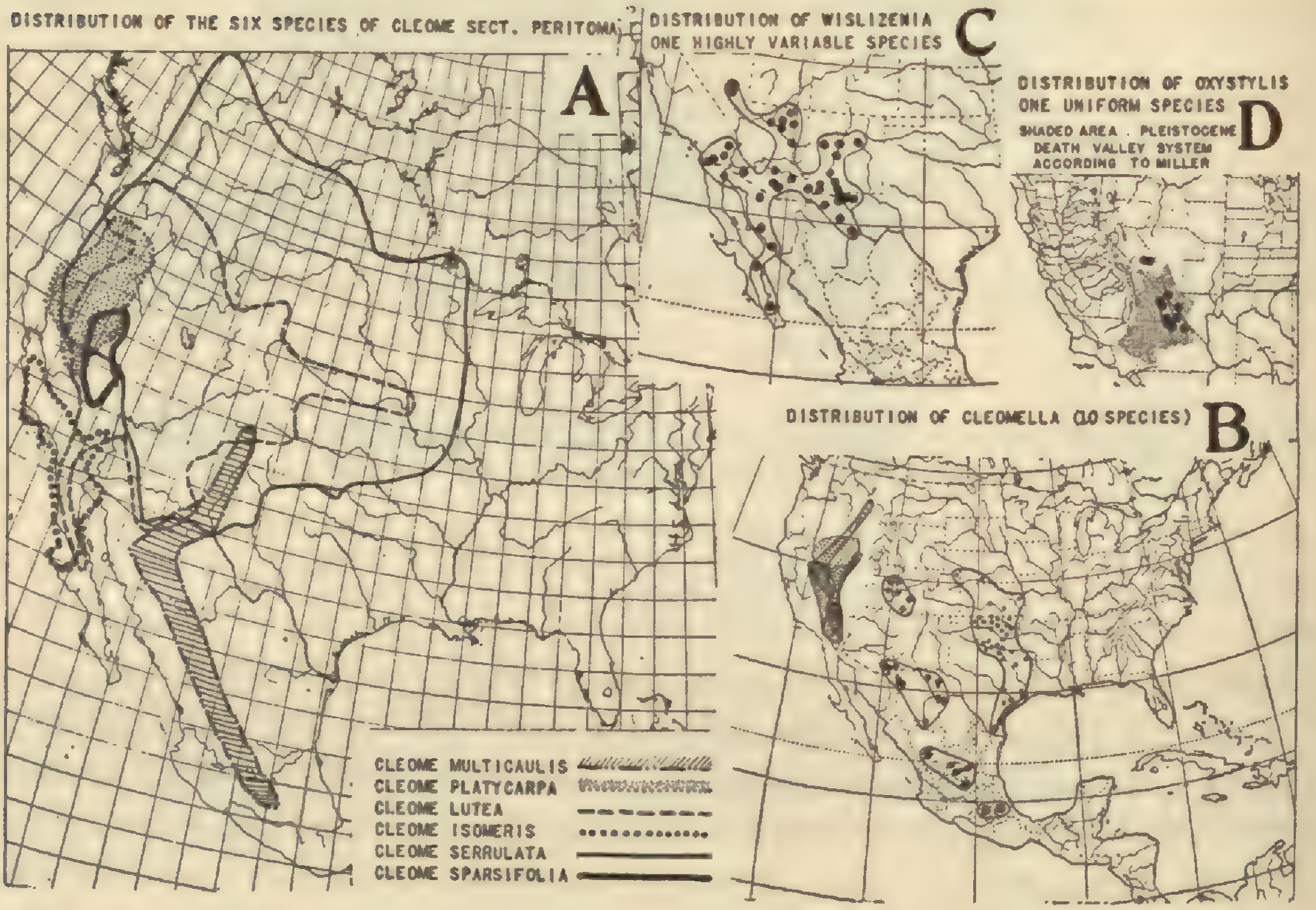

Fig. 12. Distribution of all taxa in the western North American Cleomoideae and the degree of sympatry and allopatry in each genus.

an environment fast changing to a more xeric one will evolve rapidly. The other part, if its environment does not markedly change, may remain more generalized and will evolve slowly. Generally, the more primitive taxa (subspecies, species, genera) will be found in the more mesic climates, the more specialized in more xeric ones. If two taxa have thus evolved from one original population through geographic isolation they would *at least for a time* occupy allopatric ranges. By deciding which of the two related taxa is more specialized and which more primitive we can speculate on the geographic direction of evolution and on the geographic origin of taxa. That such a scheme is applicable only to relatively recent evolution need not be emphasized (cf. Deevey, 1949).

Wagner's ideas as amplified in "Jordan's Law" or "Rule of Proximity", that "given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort" (Cain, 1944), has been found to apply chiefly to species or subspecies within the same genus. The fact that it apparently also applies to related genera, or to closely related species, one in one genus and one in another, greatly extends Jordan's Law. However, such complementary ranges appear here too frequently to be accidental. In the western North American Cleomoideae, the geographic ranges of the two most closely

related taxa of two related genera or, sometimes, the total ranges of two related genera, are highly allopatric, a trend that appears congruent with the phylogeny as outlined on morphological grounds.

Cleome.—The geographic origin of the genus *Cleome* is unknown, though the apparently primitive species occur in the New World tropics. Sect. PERITOMA is similar to some New World *Cleome* species and apparently has been derived from them. The occurrence of *C. multicaulis* in central Mexico (fig. 12A) suggests that section PERITOMA as a whole originated in the Mexican highlands, one of the two important distribution centers of *Cleome* in the New World (the other being South American), the area from which Madro-tertiary elements of the southwestern flora appear to have originated (Munz, 1935; Chaney, 1947; Axelrod, 1948). The total range of PERITOMA is allopatric to that of the other sections[15] of *Cleome* (fig. 13A).

In spite of the fact that the range of PERITOMA overlaps that of *Cleomella* nearly completely (fig. 9), offering little help in tracing the origin of *Cleomella,* we can profitably compare the ranges of the most *Cleomella*-like species of *Cleome* sect. PERITOMA *(Cleoma lutea)* with those of the most *Cleome*-like species of *Cleomella* (the midwestern *Cleomella angustifolia* and the Mexican *C. longipes*). All are very much alike in habit, inflorescence, and seed structure. *Cleome lutea* is clearly allopatric to both species of *Cleomella,* although its range nearly touches theirs in two places (fig. 13B).

The range of *Wislizenia* complements that of *Cleomella* (fig. 13C) except for a major overlap in northern Mexico and adjacent New Mexico and Texas. The two most closely related taxa of the two genera are *Cleomella longipes* and *Wislizenia r. palmeri* (a southwestern, primitive variety). Both are allopatric, being separated by the northern Sierra Madre Occidental. We can postulate, as shown by arrows in fig. 13C, that *Wislizenia* originated in western Sonora, from a branch of *Cleomella* (similar to *C. longipes* ?) isolated by the rising Sierras, and subsequently migrated north and east. Eventually, as *W. r. refracta,* the genus spread through the wide gap of the continental mountain axis in southern Arizona and New Mexico, thus reentering the territory of its ancestors *(C. longipes)*, where the two genera are now sympatric.

Wislizenia and *Oxystylis* are exactly allopatric (fig. 13D), their dividing line the "Death Valley drainage-Colorado River drainage" watersheds (Miller, 1950; Hubbs and Miller, 1948). *Wislizenia,* to my knowledge, has never been collected or reported from the Death Valley region (Coville, 1893, and others).

The above data suggest the origin of these genera as follows (fig. 13A–D): *Cleome* sect. PERITOMA evolved from a mesophytic Mexican *Cleome.* In some drier regions, perhaps in northern Mexico, southern Arizona, New Mexico or western Texas, one of the taxa of *Cleome* (*C. lutea* ?) gave rise to *Cleomella* which

[15] Except for the unifoliolate species and *Cleome tenuis* Wats., which belong to a section (to be named in the near future) more closely related to Old World taxa than to any of the New World.

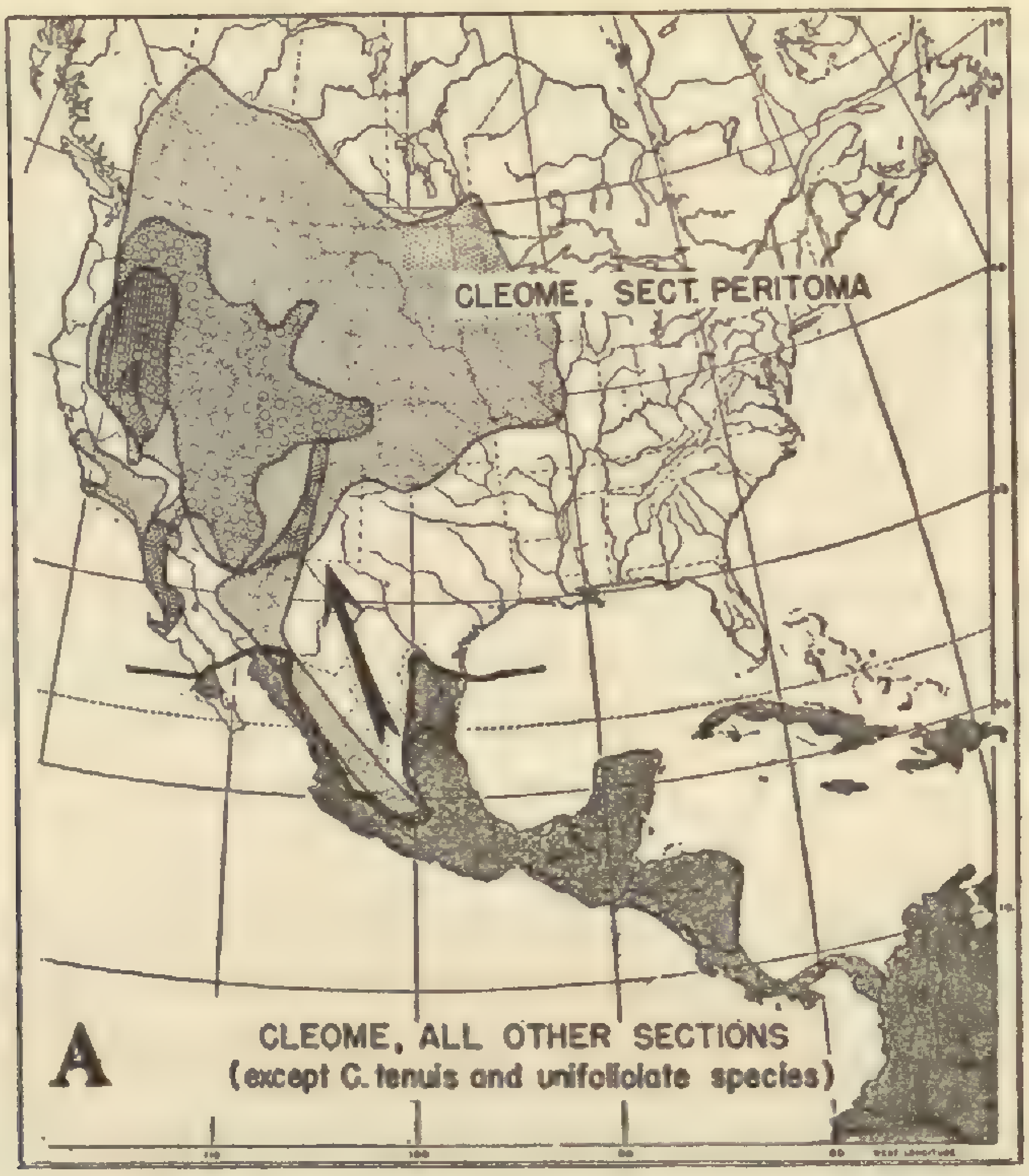

Fig. 13. Geographic distribution and origin of genera. Arrows point from the less specialized to the two most closely related taxa, one in one genus and one in the other.

spread and evolved into many species. The more primitive species apparently remained in the mesic regions with little climatic change, while the more specialized evolved mainly in the California and Nevada deserts and in the Mexican plateau (Iltis, 1956). A southwestern primitive population of *Cleomella* (*C. longipes* ?) spread to Sonora and California and evolved into *Wislizenia* which, spreading north and east, evolved a number of variants. One of these (*W. r. melilotoides* ?) became isolated in the Death Valley region, where it evolved into *Oxystylis*.

Although the center of variation (region with the most genera or species) for the western North American Cleomoideae lies within southern California and Nevada, their putative centers of origin appear to be more to the southeast. This supports Cain's (1944) contention that the two types of generic centers are not necessarily synonymous.

VI. Degrees of Inter-Generic and Inter-Specific Relationship and Intra-Specific Variability

Any systematist knows that there are different kinds of genera, just as there are different kinds of species. These differences between genera are in part due to variations in: (1) the degrees of inter-generic relationships within a group of closely related genera; (2) the degrees of inter-specific relationships; and (3) the intra-specific variability.

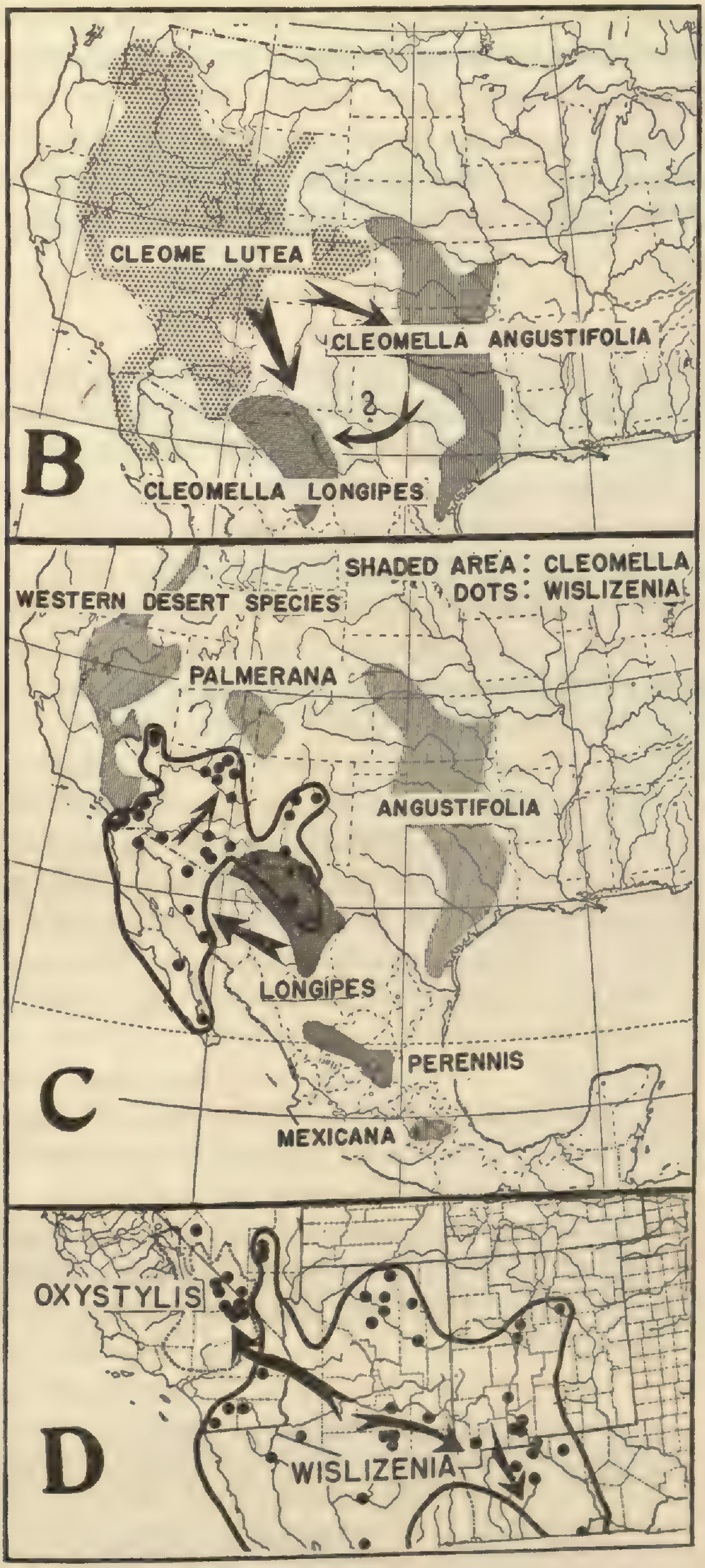

Fig. 13 (Continued). Heavy line in D encloses the Death Valley drainage system.

We can ask: (1) How closely are the genera in the group related to one another?; (2) How closely are the species in one genus related to each other?; and (3) How much does each species vary?

For the taxa dealt with in this study, at least, the answers to these questions fall into well-defined patterns and correlate with the phyletic series previously discussed as well as with the geographic distribution and therefore prove significant to phylogeny.

(1) *Degrees of Inter-generic Relationships.*—

Cleome can be considered the "mother genus," the *genus primordioides* or *primitivus* of the Cleomoideae (Buxbaum, 1951), from which all other genera in the subfamily, the *genera progressiva,* have been derived. Whatever primitive relatives *Cleome* still may have, they must be sought in the Capparidoideae[16] or, preferably in other families. As the primitive genus, *Cleome* contains the least specialized taxa within the subfamily as well as a considerable number of specialized ones that cannot be segregated conveniently from the primitive generic plexus. Thus, the natural section PERITOMA can be thought of as a specialized branch within the genus, a contention which is supported by the allopatry of PERITOMA with respect to the other sections of *Cleome* (fig. 13A).

The exact position of PERITOMA within *Cleome* is not certain. The fused claws of the seed, the closed, convolute aestivation, and other characters indicate a fairly close relationship to the other New World species of the genus. Although the species of PERITOMA do not differ from these by any outstanding qualitative characters, they do differ in the way they combine various characters which occur in diverse groups of *Cleome.* Hence, a generic segregation of PERITOMA from *Cleome,* although natural, would be impractical, though McVaugh (1945) has made just such a recommendation for this type of situation.

Cleomella is exceedingly close to *Cleome* sect. PERITOMA. Biologically, it is nothing but a specialized segment of the PERITOMA plexus which, because of its short, transversely expanded fruits, can be easily segregated. While there are two rather tenuous, quantitative differences between the two genera, the only qualitative difference, and then not an absolutely constant one, is the transverse expansion of the valves. If the fruit of certain, quite unrelated, South American species were placed in this sequence (e.g., *C. siliculifera* Eichl., fig. 1D) there would be no way of telling where one genus begins and the other ends. However, in North America, the break between *Cleomella* and PERITOMA is fairly sharp, and *Cleomella,* a useful genus, is undoubtedly also a good biological unit.

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[16] The members of this subfamily are shrubs and trees of the tropics; in nearly all characteristics of fruit and seed, as well as in many flowers and leaves, they appear to be, if anything, more *specialized* than the Cleomoideae, from which, contrary to current opinion, they may have been derived.

Wislizenia has close affinity with *Cleomella,* although it is not as close as between *Cleomella* and *Cleome,* with *at least* three quantitative differences (reduction of seeds, bracts, replum) and one complex, qualitative difference (shape and ornamentation of the fruit) to separate the genera.

Oxystylis differs sharply from *Wislizenia* by *at least* three quantitative characters and two qualitative ones (extreme modification of replum; telescoped inflorescences).

Assigning one point for each "simple" quantitative inter-generic difference and two points for each qualitative difference, the morphological discontinuity between any two genera follows a trend from *Cleome* to *Oxystylis,* with three points or less between *Cleome* and *Cleomella,* about five points between *Cleomella* and *Wislizenia* and seven or more points between *Wislizenia* and *Oxystylis.* Although this arbitrary point system takes into account only the more obvious characteristics, the relative values are essentially correct as shown by fig. 1. This progressive increase of inter-generic difference, approximately represented by the numbers 3–5–7, suggests some accelerative type of evolution which will be discussed toward the end of this paper (cf. fig. 15B).

(2) and (3). *Degrees of Inter-specific Relationships and Intra-specific Variability.*—
Cleome sect. PERITOMA is composed of six species so very distinct that some botanists have deemed it necessary to establish segregate genera for them: *Isomeris* Nutt. (for *C. isomeris*); *Carsonia* Greene (for *C. sparsifolia*); *Peritoma* Nutt. (for *C. lutea, C. serrulata,* and *C. multicaulis*); and *Celome* Greene (for *C. platycarpa*).

Variability within the species of *Cleome* is not uniform. Some, such as *C. platycarpa, C. multicaulis* and *C. sparsifolia,* all taxa with comparatively small ranges, are monomorphic. Others, such as the widespread *C. serrulata* and *C. lutea,* vary considerably, mainly in silique shape and length. *Cleome lutea* is the only species easily divisible into geographic varieties, with *C. l. lutea* widespread and *C. l. jonesii* Macbr. occurring from central Arizona to Baja California. That this divisible species is also the most primitive taxon of PERITOMA is significant. *Cleome isomeris,* highly variable in fruit shape, has been divided into three geographic varieties which overlap and intergrade and are difficult to maintain.

The ten species of *Cleomella* are more closely related to ane another and compose a more tightly-knit group than do the six species of *Cleome* sect. PERITOMA. Flowering plants of different species of *Cleomella* sometimes are almost indistinguishable, a situation not encountered in PERITOMA. Great variability in fruit shape or in pedicel and gynophore length is characteristic of some species, as in the relatively widespread *C. plocasperma* or the more local *C. palmerana* and *C. obtusifolia.* Most other species are monomorphic (Crum, 1929; Iltis, 1955b, 1956). No species is divisible into geographic varieties.

Differences of opinion regarding subgeneric (i.e. subspecific) divisions within *Wislizenia refracta sensu lato* are due largely to the great variability in shape, size,

ornamentation and divergence of fruiting valves and in the length of the raceme. While the specialized smaller-fruited, obovoidal- and smooth-valved plants generally occur in the eastern *(W. r. refracta)* and northern *(W. r. melilotoides)* parts, and the primitive larger-fruited, obconical- and spiny-valved plants (var. *palmeri*) in Baja California and Sonora, the variability does not lend itself easily to taxonomic resolution. The many local races apparently replace each other complementarily (Greene, 1906), without much of a break in morphological pattern. Ten species of *Wislizenia* have been described to date (Greene, 1906). Jepson (1936) considers all, except *W. palmeri,* as varieties of *W. refracta.* I. M. Johnston (1924) interprets the genus as monotypic and very variable, recognizing three geographic varieties, while Crum (1929) considers the primitive and specialized extremes and the intermediates as separate species, all subdivisible into a number of weak varieties. *Wislizenia refracta sensu lato* is indeed highly polymorphic. It deserves to be studied by the methods of modern systematists.

Specimens of *Oxystylis lutea* are not common in herbaria and information about its variability rests on meager evidence. I have examined sixteen different collections, usually several plants in each; it is doubtful whether very many more have ever been made. If there were any appreciable variability among them it was not apparent.

VII. Discussion

Any phylogenetic interpretations of the facts of morphology, geography and variability are highly subjective. In the words of Lam (1951) they "*may* have evolutionary significance, but . . . represent *no* phylogeny, for the simple reason that these schemes are always one-time schemes, with no fossils whatever involved". A different viewpoint, stressing the value of phylogenetic series to the understanding of taxonomy, is that expressed by Buxbaum (1951), with whom I concur.

1. *Correlation of Geographic Distribution and Intra-generic Relationships with Morphology to Determine the Relative Age of a Genus.*—

The fruit, raceme and stipule morphology indicates that *Cleome* is the primitive member of this sequence and that *Oxystylis* is the most advanced; in other words *as genera Cleome* is the oldest and *Oxystylis* is the most recent. The direction of evolution is thus inferred and the relative age of each genus is implied on morphological grounds. Is it possible to correlate patterns of geographic distribution and degrees of intra-generic relationships with the morphological evidence?

The distinctiveness of species in *Cleome* sect. PERITOMA indicates that we are dealing with very old taxa. The species, as we know them, may be young, but the point of divergence of the evolutionary lines that have given rise to these species dates far back in time. Not only are these species very distinct morphologically, but the high degree of sympatry in the group indicates they must also be very distinct genetically (fig. 12A, 13A), for in many places two or three species grow side by side without the slightest indication of hybridization or introgression. For

instance, in the alkaline semi-deserts of the San Luis Valley of southern Colorado, *Cleome serrulata* and *C. multicaulis*, the only species in the section with purple flowers and, in some ways, closely related, grow together with branches intermixed and flowers often touching. Yet, despite careful searching, there was no evidence of hybridization. At Vernal, Utah, *Cleome serrulata* and the very similar *C. lutea* grow in abundance on the same slope. Mass collections by Edgar Anderson show no evidence of introgression!

It is almost axiomatic to declare that sympatric species, as a rule, are old. They have to be, for only after prolonged isolation are two sibling species likely to be sufficiently differentiated that they can exist side by side without re-merging. Therefore, geographically evolving populations have to be allopatric before they can become sympatric (Mayr, 1942).

One would expect then that the genus *Cleomella*, with a *Cleome*-like group as its morphological prototype, would be younger than *Cleome* in other ways as well, and that this age difference would be reflected in the geographic distribution of the species. A glance at fig. 12B shows that this is true. Of the ten species of *Cleomella*, five are allopatric and five are more or less sympatric. As one would also expect in a younger genus, the species of *Cleomella* are usually much more closely related to each other than are those of *Cleome*. Also, the ranges of some of the allopatric species (e.g., the Mexican taxa) still bear the earmarks of having evolved from a once-widespread species through disjunction and subsequent differentiation (Iltis, 1956).

The hypothetical wide-ranging species differentiating into smaller units has passed out of existence in *Cleomella*. However, it is well-exemplified by the "super-species" *Wislizenia* which in its distribution is in a younger stage of evolution (fig. 14). The genus has a single widespread species with a scattered but not markedly disjunct range (fig. 12C). It is highly polymorphic, each of its many populations differing from the next only in minutiae. One series of populations, the southwestern var *palmeri*, is morphologically distinct enough to be called a variety, a subspecies, or, by some, even a species. Most of the other local races are so similar to each other that they have not always been dignified with even supspecific recognition. In studying the diverse fruits, one can almost "see" this species in an active stage of evolution, differentiating into smaller, more local units. Since these populations appear to replace each other geographically, the intraspecific (i.e. intra-generic) allopatry is complete.

Oxystylis, the most specialized and advanced genus morphologically, is youngest in its distribution-variation patterns. With one possible exception, its range is nearly continuous, and the variability within its single species negligible.

The following table gives the number of species in each genus with overlapping ranges (per cent of sympatry).

The sequence is quite clear: from the primitive genus with large, overlapping ranges and very distinct species, through the next genus with smaller, partly over-

lapping, partly separated ranges and more or less closely related species, through the third genus with small allopatric ranges of closely related populations, to the last, most specialized genus *Oxystylis,* where the single species is so uniform morphologically that ranges for individual populations cannot be plotted.

If we start the sequence *backwards* from the youngest to the oldest, we can, in a sense, "see" the evolution of a genus exemplified by the accompanying conceptual scheme (fig. 14). Thus, a genus would have to start in an *"Oxystylis"* stage to get to a *"Cleome"* stage.

Genus	Number of species	Per cent of sympatry	Kinds of taxa
Cleome 6 spp.	1 sympatric with 1 species 1 " " 2 " 2 " " 3 " 1 " " 4 " 1 " " 5 "	17 33 50 67 83	Species exceedingly distinct; ranges often large or medium
Cleomella 10 spp.	5 sympatric with no species 1 " " 2 " 2 " " 3 " 2 " " 4 "	0 20 30 40	Species distinct to very closely related; ranges medium to small
Wislizenia 1 sp., 3 or more subsp. divisions	1 sympatric with no species	0	Taxa (populations and geographical varieties) closely related; ranges small and local
Oxystylis 1 sp.	1 sympatric with no species	0	Taxa (populations) uniform; ranges of individual populations cannot be delimited on morphological grounds because of uniformity

2. *Willis's "Age and Area".*—

When the ranges of all four genera are plotted on the same map (fig. 9), they are seen to *roughly* follow a pattern of what has been called "progressive equiformal areas". Centering essentially around the range of *Oxystylis,* the ranges of *Wislizenia, Cleomella,* and *Cleome* sect. PERITOMA become progressively larger. Such a pattern seems, on the surface, to fit perfectly into Willis's (1922) ideas of "Age and Area". According to this theory, the youngest genus, *Oxystylis,* would occupy the smallest range because it has had little time in which to spread its seeds; the oldest genus, *Cleome,* would occupy the largest range because it has had eons of time in which to spread from its original home.

This reasoning, however, does not apply to the situation in the Cleomoideae. A comparison of this distribution map with some generalized climatic maps will reveal

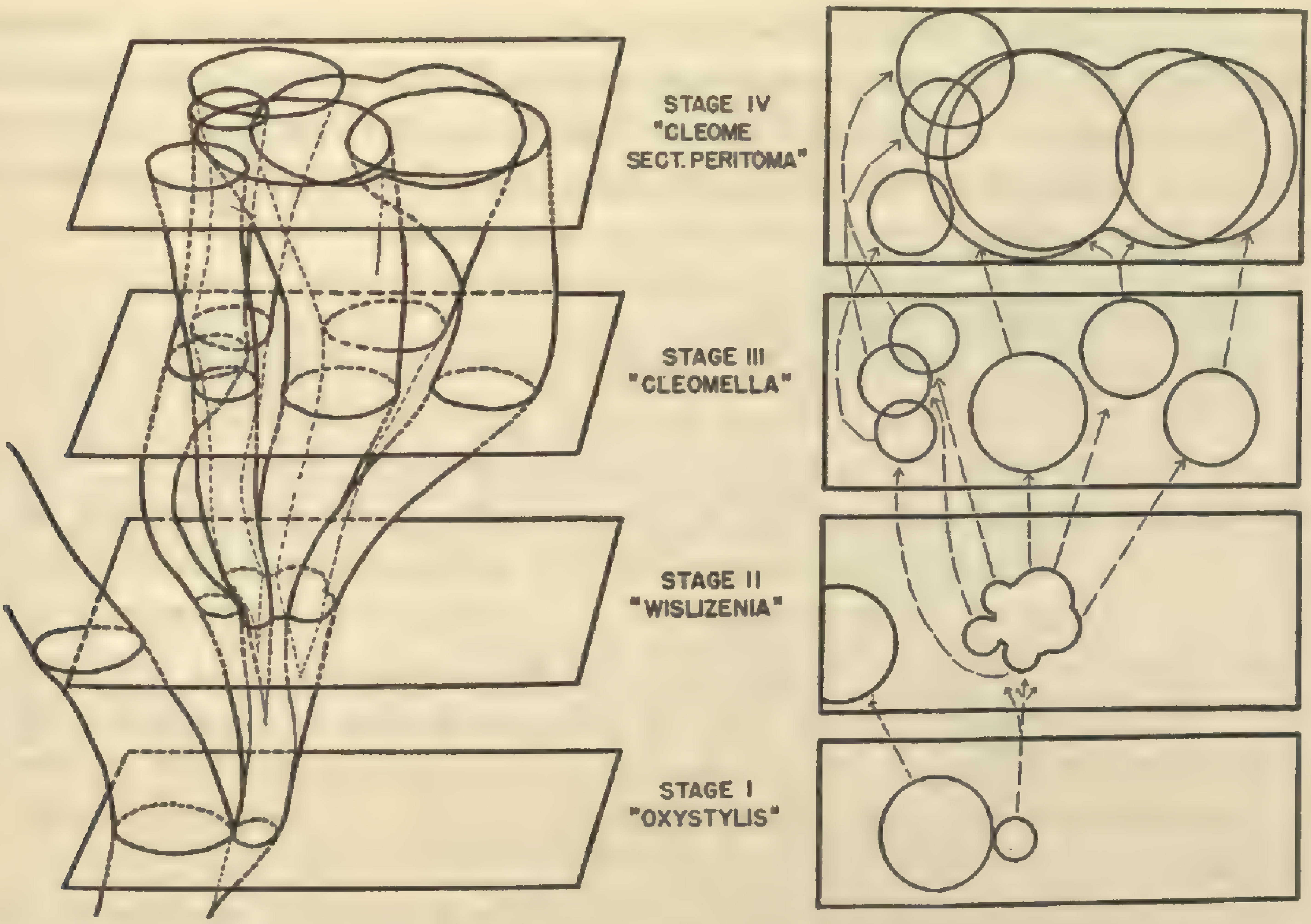

Fig. 14. Hypothetical scheme showing stages in the geographic evolution of genera as exemplified by the four genera of western North American Cleomoideae. Explanation in text.

that the primitive *Cleome* usually occurs in more mesic regions and that the ranges of *Cleomella, Wislizenia,* and *Oxystylis* are progressively more restricted to regions of greater aridity.

Since only those plants adapted to aridity were selected, the plants with "mesic" genes tended to be eliminated by progressively more arid environments. By the time such a highly modified plant as *Oxystylis* had been produced by the narrow channels of selection, its genotype had been shorn of all but "super-xeric" genes, producing a homogenic species (Stebbins, 1942). Its range is small, not because of the limited time in which its seeds could have been disseminated, but because of its narrow physiological tolerances. Selection produced a highly specialized plant, not only morphologically but physiologically and ecologically. Plants of *Oxystylis,* being biotypically poor, are literally the "prisoners" of their own genes. This is also true of the other genera, but less so. Most species of *Cleome* sect. PERITOMA are widespread but they have their limits, for none are native in the moister, wooded regions east of the Mississippi. In general, morphological conservatism is matched by relatively great physiological (ecological) tolerance; morphological specialization by physiological intolerance (specialization).[17] This statement applies to the over-all generic ranges as well as to specific ranges; thus, the most highly special-

[17] At least "immediately" following the evolution of the particular morphological specialization. That readaptation to mesic environment with retention of morphological specializations could follow, seems reasonable and has been discussed by Stebbins (1952).

ized taxa, *Cleome sparsifolia, Cleomella obtusifolia* var. *taurocranos, C. brevipes, C. parviflora*, etc., *Wislizenia refracta* var. *melilotoides*, all occur in the vicinity of *Oxystylis* (although not in Death Valley). Likewise, *Cleomella mexicana*, the most specialized of a phylad of three species, is restricted to the vicinity of two salt lakes in central Mexico (Iltis, 1956).

3. *The Probable Age of Oxystylis.*—

Since *Oxystylis* is apparently an indigenous endemic (Sinnott, 1916) of the Death Valley region and the range of its closest relative is allopatric to the south, it can be deduced that it is a highly specialized northern segment of *Wislizenia* which became isolated and *evolved in Death Valley*. The physiography of the region (fig. 13D) suggests this strongly, for the contemporary watershed between the Colorado and Death Valley drainage systems (Miller, 1950) corresponds exactly to the line between the ranges of *Oxystylis* and *Wislizenia* (fig. 12). Furthermore, Miller (1946) postulates, on the basis of fish distribution and geologic evidence (Blackwelder and Ellsworth, 1934), that there was once a connection between the two basins in that area and that it may have served as a migratory route for *Wislizenia*.

Death Valley functions as a kind of island whose isolation, together with the extreme climatic conditions, evidently furthered speciation. This is supported by the considerable number of endemic taxa known from there, both plants (Munz, 1935; Dressler, 1954; Tryon, 1955 [*Selaginella leucobryoides*]) and animals (Miller, 1950), which appear to be indigenous endemics usually with southern affinities that *evolved* from relics of once more widely distributed taxa (apparently not plain relics as Miller states). Living in that region, they must be adapted to its *present-day* climate of extreme heat and drought. If these adaptations originated *in situ*, they are probably recent, since, as Parish (1930) phrases it, Death Valley and the Mojave Desert had once a "greener youth," for "there is abundant evidence that in the Pleistocene Age, perhaps 20,000 years ago, this whole region enjoyed an abundant rainfall, and—as a necessary sequence—must have had vegetation very different in its character from that which prevails today." Many authors (Campbell and Campbell, 1937; Antevs, 1937; Miller, 1946; Hubbs and Miller, 1948) present strong evidence that the whole region of eastern California was one of large, deep lakes in the late Pleistocene or even more recently. Blackwelder and Ellsworth (1934) think that an immense Pleistocene lake filled Death Valley, whose waters overflowed to the south into troughs that eventually emptied into the Colorado River. Miller (1946) names the integrated river system of that time the "Death Valley system" because the Death Valley formed the sump for its waters. According to Antevs, the lakes probably date from the last pluvial period, between 20,000 and 25,000 years ago, and Lake Mojave may have been at its fullest as late as 15,000 years ago. Indians then lived in this region (Campbell and Campbell, 1937, and others in same symposium) which, in its aridity and alkalinity, is now desolate and forbidding to human habitation.

It is unlikely that *Oxystylis*, or its ancestral forms similar to *Wislizenia*, were able to grow in Death Valley during this moister period! It is also unlikely that *Oxystylis* or its ancestors migrated to Death Valley from other places than those to the south, since the northern regions were then even cooler and moister than they are now. There is furthermore no evidence that *Oxystylis* has ever grown outside its present range. "The distribution of the existing Flora of California indicates that the majority of the endemic species originated in their present area" (Campbell and Wiggins, 1947). Instead, we might postulate that the *Wislizenia*-like ancestor of *Oxystylis* migrated north *after* the Death Valley region had become about as arid as the habitats in which *Wislizenia* grows now and that the evolution of *Oxystylis took place within Death Valley in the extremely short time of 15,000 years or less.*

Fifteen millenia for the evolution of a genus seems short indeed, even for the evolution of a species under most circumstances! According to Mangelsdorf (1952):

> Evolution is usually regarded as a process which moves with majestic and unhurried pace through geological periods . . . whose progress is measured in millions of years . . . and which . . . is ordinarily thought of as so slow that even the second hand on the evolutionary clock does not travel perceptibly in the span of a human lifetime or, in many cases, during the period of recorded human history.

In some areas and in some taxa the "evolutionary clock" has practically stood still for a tremendous time span as, for example, in the temperate mesophytic wooded regions of the southeastern United States and eastern China. In many genera, the differentiations that have occurred there since the late Eocene or Miocene, 30 million or more years ago, have been on specific, varietal or even lower levels (Cain, 1943; Sharp, 1951; Li, 1952). Yet, as Mangelsdorf and others find exception to this condition in the very rapid evolution of animals and plants under domestication, we may postulate exceptions in organisms, particularly annual plants, which live in arid environments or which find themselves in environments changing rapidly toward aridity.[18]

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[18] Xerophytic and cultivated plants have certain similarities as to environment and evolution. Both occur frequently in full sunlight and in mineral soils. Both are often annuals, in which evolution has been most rapid. Both favor open habitats with little inter-specific competition. For cultivated annuals, the habitat is kept open artificially by weeding and plowing. In annual xerophytes, the habitat is also open in the sense that: (1) a desert wash or playa is often disturbed and disrupted naturally, with bare gravel and sand a result of sporadic periodic hard floods; and (2) annuals being the characteristic plants of a desert, their habitat is not closed or preempted at the beginning of the growing season by plants already there, as in a sedge meadow or forest which has a very high number of vegetatively reproduced perennials. Thus the amount of successful germinations in deserts is often very great in a good season, the nearly pure patches of certain species resembling those of cultivated plants. As in a field of cultigens where lack of interspecific competition is conducive to the survival of all genotypes planted, so in a good season the mutants as well as the standard forms of desert annuals are apt to survive, while in a dry unfavorable season those "odd" morphological types better adapted for germination requirements will be selected for and will predominate. This phenomenon may be compared to the practice of taking two heads of wheat out of 10,000 to start a whole strain, which partly accounts for the rapid evolution of cultigens. The desert environment, which periodically allows only a few favored seeds to grow in an open habitat, may appreciably alter the genetic constitution of a population in a few generations, thereby accelerating the evolutionary rate.

4. *Arid Environment and Rapid Evolution.*—

That dry and hot environments favor more rapid evolution than do mesophytic organisms, for example, has been substantiated by studies on fossil and recent organisms as well as on theoretical grounds (Muller, 1942, and Stebbins, 1947, 1949, for plants; Miller, 1950, for fishes of desert hot springs). This seems to be due to the following factors (Stebbins, 1952): (1) Ecological fragmentation of habitats, and therefore populations, in arid regions is much more pronounced than in mesic ones, thus producing many situations favoring isolation and consequently speciation. With climatic fluctuations one can expect rapidly changing selection, and with the remerging of habitats and populations, introgression. (2) The fragmentation of the habitats produces large or medium-sized populations with isolated subunits interchanging genes only occasionally, a situation most favorable to genetic drift and therefore to rapid evolution. (3) The number of special adaptive structures that can be produced in these environments may be, and often is, very large; (4) the selective pressures are very high because of the extreme climate; and (5), in annuals only, the brevity of the life cycle and the rapid multiplication of generations would increase the evolutionary rate (Sinnott, 1916).

A factor not mentioned by Stebbins, but discussed for fishes by Miller (1950), is the increase in mutation rate due to direct influence of heat. Very little experimental evidence is available on this subject. Navashin (ex Babcock, 1947) reported that the mutation rate in resting seeds of *Crepis tectorum* was accelerated by increased temperatures. Shkvarnikov and Navashin (1934) found that when resting seeds of *C. tectorum* were exposed to temperatures of 54° to 55° C. for 20 to 44 days, the surviving seedlings showed chromosomal abnormalities, particularly translocations, and an increase in the mutation rate. They call attention to the fact that since heat is widely distributed in the world, it may play a considerable role in the production of mutations; and that resting seeds are often exposed to temperatures equal to or higher than those used in their experiments. This work is not mentioned in "Temperature and Evolution" (Plough, 1942, and others in same symposium) which summarizes evidence, mainly from *Drosophila*, that high temperatures (Muller 1928, 1942), as well as temperature shocks (a distinct phenomenon!), increase mutation rates. Fankhauser (1942), working with *Triturus*, showed that extreme temperatures in the laboratory induce polyploidy, and he suggested that heat might produce polyploid individuals in nature.

That resting seeds of Cleomoideae, particularly *Oxystylis*, are exposed to extreme heat is evident, considering that Death Valley shade temperatures may be as high as 134° F. and soil temperatures certainly much over 160° F. Temperature shocks may be provided in the tremendous diurnal fluctuations which, because of low humidity, are rather typical of deserts.

Miller (1946, 1948, 1950) studied the effects of desert habitats on the evolution of Death Valley fishes. He concluded that if Lake Manly (the Pleistocene Death Valley lake) was correlated with the Tahoe stage of glaciation as postulated by

Blackwelder, the two Death Valley sibling species of *Cyprinodon*, now separated by 75 miles but originally of common ancestry, have probably been isolated for about 20,000 years. These two species live in comparatively stable habitats and are not exposed to as great fluctuations and extremes of temperature as land plants, yet they differentiated specifically in only 20,000 years. He believes (1950) that in warm spring populations, high temperatures accelerate the time rate of evolution by increasing the mutation rate as well as the number of generations per year. Although he deals with fish, his evidence seems compatible with this study.

5. *Relative Age of Genera and Relative Rates of Evolution.*—

Evidence from morphology, distribution, etc. all point to the relatively old age of *Cleome* sect. PERITOMA and the progressively greater youth of *Cleomella, Wislizenia*, and *Oxystylis*. The phyletic divergence of *Cleomella* from PERITOMA must therefore date further back than that of *Wislizenia* does from *Cleomella*, which in turn must have occurred before the divergence of *Oxystylis* from *Wislizenia*. If we assume in the evolution of each genus an equal evolutionary rate (an uncalled-for assumption!), we would expect (fig. 15A) the greatest morphological gap between the genera separated for the longest time (*Cleome* and *Cleomella*) and minor morphological differences between the genera which had diverged most recently (*Wislizenia* and *Oxystylis*).

The situation is, however, exactly the reverse! Inter-generic differences are greatest between *Wislizenia* and *Oxystylis*, and only very slight between *Cleome* and *Cleomella*. The relative morphological discontinuities between the genera were found to be about 2 to 3 points between *Cleome* and *Cleomella*, about 5 points between *Cleomella* and *Wislizenia*, and 7 or more points between *Wislizenia* and *Oxystylis* (fig 15B). Evidently, over-all rates of evolution were *not* uniform, but increased with the formation of each new genus. *Cleomella* evolved relatively slowly, *Wislizenia* faster, and *Oxystylis* most rapidly.[19]

This "speeding-up effect" of arid habitats on evolution is consistent with the generalizations of Stebbins (1947); namely, that "rapid evolution requires: (1) the presence of a rapidly changing environment" and (2) a group of plants "preadapted in the direction of the secular change". Both of these conditions seem to apply here. Since the four genera of Cleomoideae evolved in the arid and semi-arid regions of southwestern North America, the ancestral PERITOMA branch of *Cleome* must have been preadapted to xerophytism. We also know that during the past

[19] One of the obvious and perhaps insurmountable objections to this interpretation is simply that the gap between *Wislizenia* and *Oxystylis* is great because intermediate taxa have died out. It seems more reasonable to argue for the extinction of older taxa than for that of more recent ones, since the older the taxon the greater the opportunity for extinction. However, between the oldest taxa, *Cleome* and *Cleomella*, there are only the weakest of differences and between the youngest, the most pronounced in the subfamily.

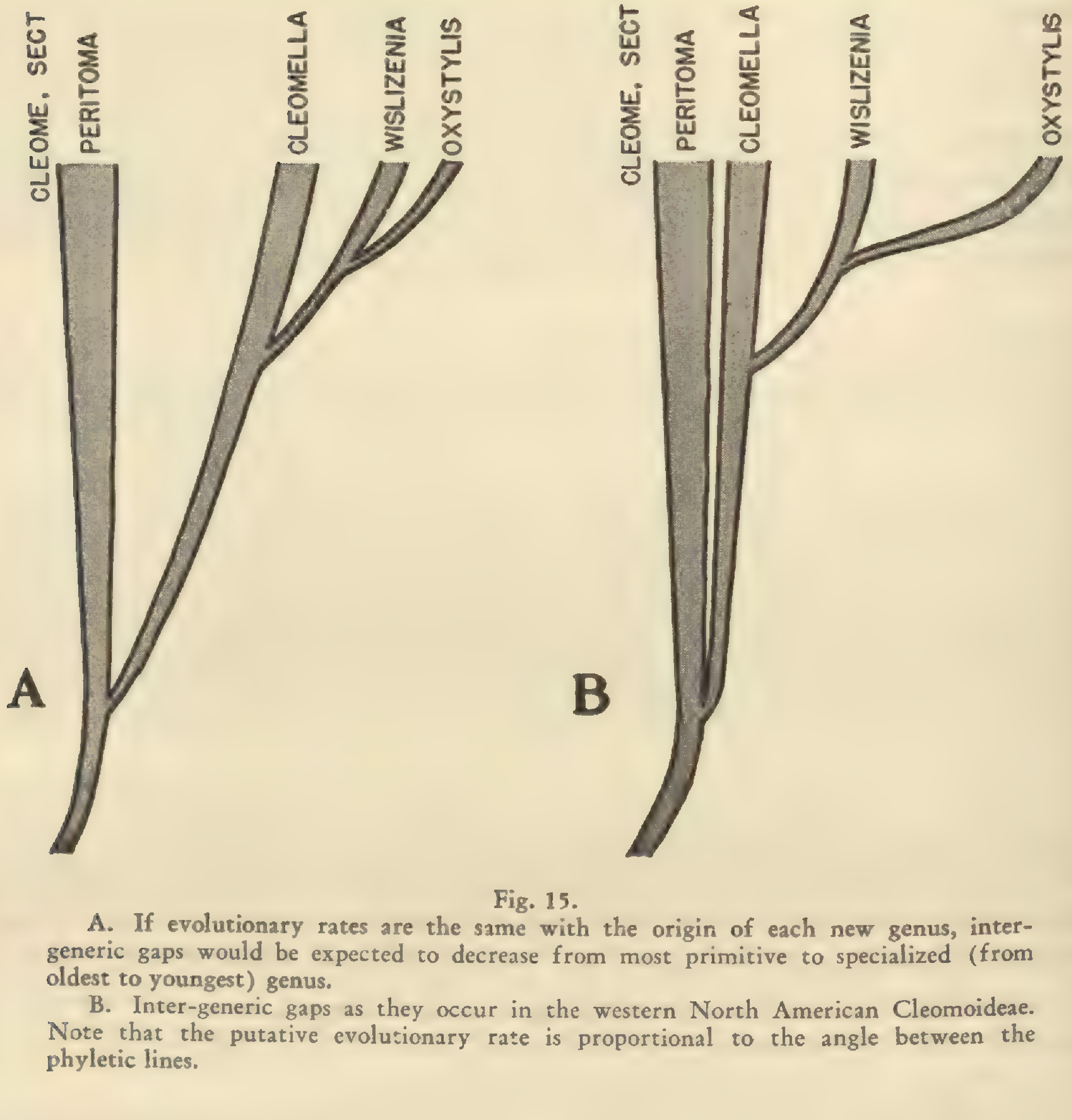

Fig. 15.
A. If evolutionary rates are the same with the origin of each new genus, inter-generic gaps would be expected to decrease from most primitive to specialized (from oldest to youngest) genus.
B. Inter-generic gaps as they occur in the western North American Cleomoideae. Note that the putative evolutionary rate is proportional to the angle between the phyletic lines.

20 million years the climate in the Southwest has oscillated tremendously from moister, subtropical in the Lower Oligocene (Chaney and Sanborn, 1933) to the initiation and development of drier and cooler grassland and desert environments of subcontinental extent. This trend progressed, with fluctuations, from warm and mild climates in the middle Pliocene (Axelrod, 1948) to the present day, except for marked interruptions during the Pleistocene, when climatic zones shifted alternately south during glacial periods and moved north during the interglacials. Since the last glacial period the change toward greater aridity has been rapid in such places as Death Valley and the Great Basin (Hubbs and Miller, 1948). This aridity is in part a result of rain shadows due to mountain building, some of which occurred as late as the Pleistocene and may be continuing today (cf. Deevey, 1949).

Cleome sect. PERITOMA may have originated during the second major burst of angiosperm evolution (Stebbins, 1947) in the middle Tertiary in the wake of climatic shifts toward aridity, either from Madro-tertiary forms that evolved in the

Mexican Plateau and moved northward, *or* from mesophytic, forest-inhabiting Cleomoideae which were left behind in the southward movement of the vegetational zones. *Cleomella*, judging from its scattered distribution in the Great Basin and east and south of the Rocky Mountains, might have had its origins also during that period. It apparently originated far east of the Sierras before their elevation in the late Pliocene, for only one of its taxa was able to reach and cross that mountain range (a putative "*pre-Wislizenia*", into western Sonora). "At the close of the Pliocene and the beginning of the Quaternary the present desert had its origin in the rain shadow resulting from the structural differentiation of the Sierra Madre-San Bernardino chain." (Cain, 1943). The ancestral "*pre-Wislizenia*", isolated from its relatives in *Cleomella* by a rising Sierra Madre, evolved into *Wislizenia*, eventually to spread north and east around the tip of the Sierra Madre, probably during and after the Pleistocene. During the glacial periods the less specialized species of *Cleome* and *Cleomella*, judging from their present great altitudinal and habitat tolerances, very likely were able to survive in approximately the same regions they occupy today; *Wislizenia* was probably restricted, as it is today, farther to the south. With the post-Pleistocene changes toward extreme aridity, the opening-up of alkaline valley floors to plant colonization and the correlated great disruption of previously existing habitats, we can postulate a northward expansion of ranges of xerophytes and an evolution that filled some of the newly available niches by producing not only *Oxystylis* in Death Valley, but also such exceedingly specialized species as *Cleomella brevipes* in the Mohave Desert, *Cleome sparsifolia* in Nevada, and the local diversification of *Wislizenia* and other species of *Cleomella*.

"Accelerative evolution" is interpretable through organism-environment relationships as postulated by Simpson (1944) and Stebbins (1949, 1950); in our case, through the obvious direct relationship of morphological specialization to habitat specialization and to evolutionary rate. We might say that mild environment would result in mild selection, the consequence of which is slow morphological or physiological evolution; a change to a progressively more arid environment would produce greater selection, resulting in faster evolution. Accelerative evolution, then, will be exhibited by semi-desert plants, or plants preadapted to arid environments, evolving into progressively better-adapted types which are able to invade (or survive in) progressively more arid regions. The result would be increased selection, mutation, etc., making invasions of still more specialized habitats possible, which in turn would intensify the processes that have been outlined.[20]

Deserts and desert evolution must have occurred on the earth for a long time. If there is one definite fact we know concerning the world's geologic past, it is that mountain ranges have formed only to be worn down and to be replaced by new chains. That mountain ranges once had rain shadows with deserts as they do today is a warranted assumption, as is the former presence of subtropical

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[20] Whether this applies generally I do not know. The steady increase in body size of the American Equids as illustrated in Romer (1949) is essentially an accelerative increase, both for the *Megohippus* as well as the *Equus* line.

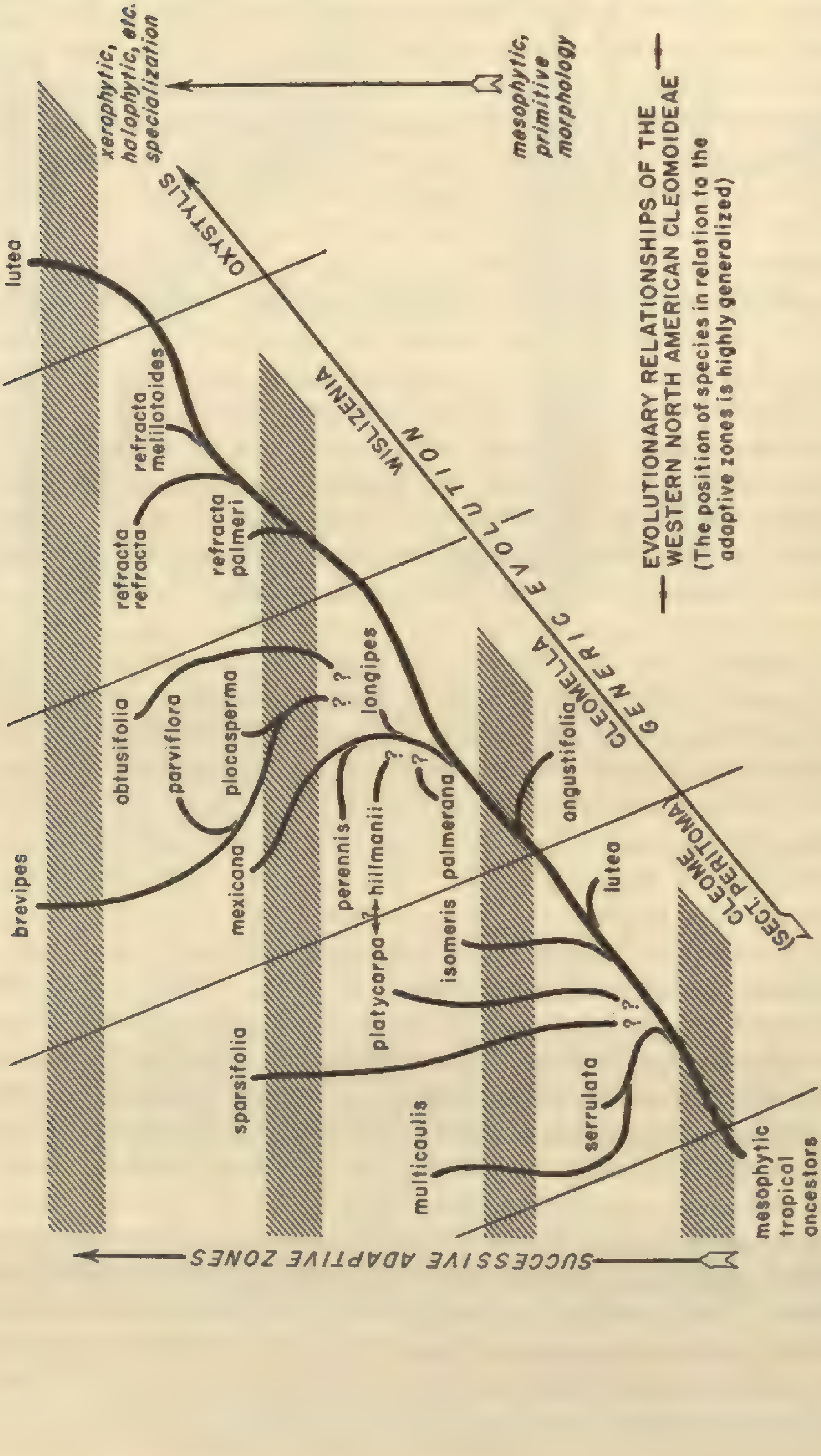
EVOLUTIONARY RELATIONSHIPS OF THE WESTERN NORTH AMERICAN CLEOMOIDEAE
(The position of species in relation to the adaptive zones is highly generalized)
GENERIC EVOLUTION
OXYSTYLIS
WISLIZENIA
CLEOMELLA
(SECT. PERITOMA) CLEOME
xerophytic, halophytic, etc. specialization
mesophytic, primitive morphology
SUCCESSIVE ADAPTIVE ZONES
mesophytic tropical ancestors
lutea
refracta melilotoides
refracta refracta
refracta palmeri
obtusifolia
parviflora
plocasperma
longipes
brevipes
mexicana
perennis
hillmanii
palmerana
angustifolia
lutea
isomeris
platycarpa
sparsifolia
serrulata
multicaulis

Figure 16

high pressure belts and their resultant arid zones. The high speed of evolution in deserts may therefore explain the problems of "macro-evolution" of the paleontologists and the seemingly sudden origin of phyletic groups from morphological types so different that they cannot be recognized by us as ancestral. This is particularly true if we assume that with reverse changes toward milder climates, rapid evolution in deserts may be followed by a reverse and slower change toward mesophytism. In some instances the "new" types of organs developed as desert adaptations may have had, by change in function and by some readjustment of structures, superior survival value to other, more ancient mesophytes. That organisms may take the circular route from mesophytism to xerophytism back to mesophytism has been documented by Stebbins (1952), and certainly has occurred again and again, in the larger sense, in the evolution of major divisions of the plant and animal kingdoms ("mesophytic" fish to "xerophytic" terrestrial quadruped to "mesophytic" whale, etc.). The general significance of such possibilities in the more recent evolutionary history of angiosperms[21] has not been fully appreciated by most evolutionists. All desert evolution was not necessarily dead end!

VIII. Summary

The four genera of western North American Cleomoideae (Capparidaceae) can be arranged in a remarkably complete phyletic reduction series, from the primitive *Cleome* sect. PERITOMA (6 spp.) through the progressively more specialized *Cleomella* (10 spp.) and *Wislizenia* (1 sp. with 3 vars.) to the highly specialized *Oxystylis* (1 sp.). The reductions run from many-seeded siliques through few-seeded silicules to two-seeded schizocarps; from open, bracteate racemes through denser, ebracteate ones to congested, ebracteate raceme-clusters; from small to very complex stipules; and from plants with much vegetative growth and delayed flowering to ones in which even the earliest leaves subtend flowers or racemes. Nearly all these reductions are interpretable as adaptive modifications, a result of selection by arid environments which favored plants with more rapid or economical life cycles.

The geographic distributions also imply that these reductions and specializations are due to adaptive evolution. The primitive forms are widely distributed in more mesic climates; the specialized have progressively smaller, essentially equiformal areas centering about the Death Valley region of California and Nevada, where *Oxystylis* is endemic. The ranges and degrees of relationship of individual taxa within each genus follow patterns corresponding to their morphology. The taxa of the primitive (therefore oldest) genus *Cleome* are all more or less sympatric

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[21] In the known fossil record, there are almost no "protoangiosperms", or even primitive ancestors, of any of the present-day angiosperm families. Angiospermy, our major phylogenetic puzzle, may perhaps be explainable as an adaptation to xerophytic life. If this be true, the lack of fossil remains might be due to extremely rapid (geologically "instantaneous") desert evolution, with the consequent short span in which widespread fossilization might have taken place, as well as the reduced opportunities for fossilization characteristic of desert habitats (in contrast to mesic or hydric habitats).

and sharply distinct, those of the more specialized genus *Cleomella* both allopatric and sympatric and less sharply distinct, and those of the monotypic, polymorphic *Wislizenia* allopatric with closely related populations. The most specialized, and therefore youngest genus *Oxystylis* is monotypic and monomorphic. The fact that there are different kinds of genera can in part be explained by differences in their age. In evolution through geographic isolation, taxa of a genus have to be allopatric before they can become sympatric, and by studying their geographic ranges and the amount of sympatry or allopatry, we can correlate geographical distribution with morphology and variability, and determine the relative age of a genus.

By extending "Jordan's law" not only to apply to the most closely related taxa within a genus, but also to a pair of monotypic genera or to the two most closely related species of two related genera, we can determine (if evolution has been geographic and sufficiently recent) the geographic direction of evolution by deciding which of the two taxa is the most primitive. Thus, *Cleome* sect. PERITOMA originated from primitive tropical species allopatric to the south. The primitive species of *Cleomella* seem to have originated from a primitive *Cleome* allopatric to the northwest. The primitive variety of *Wislizenia* is allopatric to the west of, and separated by the Sierra Madre Occidental from its putative ancestor in *Cleomella*. Finally, the most specialized variety of *Wislizenia* and its offspring *Oxystylis* have exactly allopatric ranges, the dividing line being the Death Valley basin-Colorado River basin watershed.

Since the Death Valley basin contained a series of tremendous post-Pleistocene lakes about 15,000 years ago, it seems very unlikely that *Oxystylis* migrated to Death Valley except in the form of a "*Wislizenia*-like" plant *after* a desert or semi-desert climate had become established; it is postulated therefore that *Oxystylis evolved* (1) *in the Death Valley area* (2) *within the extremely short time of 15,000 years or less.* That generic evolution at such a tremendous speed is possible under extreme selection is amply illustrated by domesticated organisms, plants and animals. Furthermore, there is a great similarity between the habitat and evolutionary rate of cultivated annuals and desert annuals. In *Oxystylis*, the rapid changes towards greater aridity resulted in extreme selection which, together with other factors characteristic of deserts, is postulated to have been responsible for this rapid evolution. To the four factors (Stebbins, 1952) which help make "aridity a stimulus to plant evolution," a fifth, the effect of extreme temperatures on the mutation rate, may be added.

The increasing inter-generic discontinuities between the four genera, represented by the arbitrary numbers 3–5–7, point to an accelerative increase in the speed of evolution with the development of each new genus. The "accelerative evolution" may be explained by an extension of Simpson's and Stebbins' postulates that in preadapted organisms, the more stringent the environment, the faster evolution, which in turn would produce better-adapted organisms able to survive in, or invade, still more stringent environments with still greater selection.

The very rapid evolution in deserts may have been of major evolutionary importance in creating radically new morphological types. With a return to mesophytic climates, some of these types may have been highly successful. Perhaps some precursors of the angiosperms, whose ancestors are as yet unknown, had their origin in desert evolution.

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STYLITES, A NEW GENUS OF ISOETACEAE

ERIKA AMSTUTZ[1]

Stylites andicola E. Amstutz, gen. et spec. nov. Isoetacearum.

Plantae amphibiae vel subamphibiae in societatibus dense caespitosis supra margines paludum alpinorum frequentes. Caudices maximi crassi apice profunde bilobi usque 7 cm. longi 1.2 cm. lati vel ultra; cortice crassiusculo fusco cicatricibus foliorum vetustorum notato; radicibus per longitudinem uno latere caudicis valde secundis usque fere 5 mm. crassis speciminum nostrorum simplicibus fortasse tandem dichotomis. Folia in rosulis densissime imbricata oblongo-lanceolata apice anguste caudato-acuminata ibique valde reflexa ca. 5.0–5.5 cm. longa 5–8 mm. lata crassa margine partis basalis aut vaginae late hyalino medio et parte apicale grosse bullato. Sporangia usque 1.5 cm. supra basem foliorum instructa oblonga ca. 5 mm. longa 2 mm. lata e foveola tenue margine indistincto proventa; trabeculis paucis paxilliformibus; velo nullo; macrosporis albidis laevibus magnitudine aliquantulum dissimilibus ca. 428–643 μ latis; microsporis non visis. Ligula anguste cordato-triangularis 3–5 mm. longa. — Nomen e στυλίτης habitore in columna derivatur caudice notabili designans.

Peru: Depto. Lima, Prov. Huarochiri, above Casapalca near Caprichosa, in alpine bogs, alt. 4750 m., 2 July, 1956, *E. Amstutz 2000* (Herb. Missouri Bot. Gard., HOLOTYPE).

These curious plants were found on a moist and limy substrate around the boggy margins of a small glacial lake near Caprichosa, a few kilometers from Casapalca, central Peru, at an elevation of 4750 m. The plants live in extremely crowded colonies forming flat and dense cushions in a belt 2–3 m. broad and about 3–5 m. from the waters of the lake. The largest colonies consist of 40 or more individual plants. Better developed specimens were found in the peripheral parts of the larger cushions (50–60 cm. in diameter).

The plants apparently are well adapted to their environment. The leaves and upper portions of the caudices are aerial, but so crowded that considerable protection from the severe environment is effected. Associates of *Stylites andicola* are sods of peat and swamp bryophyta, convex and very hard cushions of *Disticha muscoides* (Juncaceae), tufts of *Calamagrostis chrysantha* (Gramineae), etc.

These plants display several innovations which deviate significantly from the very conservative architecture of all known species of *Isoetes*. The elongate caudices are outstanding; furthermore, in digging my specimens in the frozen soil, I unfortunately failed to obtain unbroken plants, and it seems possible that the

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[1] Graduate Student, Henry Shaw School of Botany of Washington University, St. Louis, Mo.
Issued March 22, 1957.

dense cushions may actually be formed through branching of the caudices of single plants, at least in part. The fleshy roots are borne along only one side of each caudex. Here, also, my excavation was not sufficiently careful, for all of the roots were cut during the process. However, in all attached roots which remain, some more than a decimeter in length, no branching may be seen. The short broad leaves with thick and recurved tips, to which effective photosynthesis appears to be restricted, are most exceptional; but most remarkable of all is the attachment of the sporangia far above the base of the sporophylls. The fovea is extremely shallow and the sporangium is less than half included within it. The trabeculae are few and peg-like. Unfortunately, microsporangia were not observed.

Figure 1. *Stylites andicola*

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A REVISION OF THE FERN GENUS PELLAEA SECTION PELLAEA*

ALICE F. TRYON

The species included in this section of *Pellaea* are predominately Cordilleran growing in dry, rocky habitats under semi-desert conditions quite unlike those usually associated with ferns. These and most other ferns of arid regions in the New World belong to the tribe Cheilantheae of the Polypodiaceae. The revision of this section was undertaken as part of a program of study on this tribe. In the 'Genera Filicum', Copeland recognizes the genus *Pellaea* as a natural one although his remarks on the affinities of the group do not entirely support that view. A more pessimistic regard toward *Pellaea* as a genus is evident in the view of Thomas Moore some fifty years earlier for he considered it as a medley of pteroids, cheilanthoides and platylomas and stated—"*Pellaea* can only be kept up as a kind of botanical refuge for the destitute."

The section PELLAEA is a restricted but natural group based on vegetative morphology such as the nearly glabrous, imparipinnate blade and free venation, and on the continuous marginal indusium and terminal sori on discrete vein ends. Relationships with *Doryopteris*, *Notholaena* and *Cheilanthes* are not wholly clear and the final disposition of the group in *Pellaea* and with other related genera is best delayed until the entire complex can be reviewed.

The entities included in section PELLAEA under the above provisions number 15 species and 5 varieties. Within this small group there appears to be two types of speciation. Apomixis, polyploidy and hybridization have influenced speciation in *P. glabella, P. sagittata* and *P. ovata*. The series related to *P. ternifolia* seems to have evolved through gradual quantitative differentiation and through isolation of resulting populations.

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* Field work in Mexico and spore study with special reference to apogamy and evolution in desert ferns were made possible by a grant from the Bache Fund of the National Academy of Sciences.

An investigation carried out in the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Issued May 24, 1957.

Geography and Ecology

The species prevail in the southwestern United States and Mexico. *P. rufa* in South Africa is the only species belonging to this section which occurs in the Old World. Three species are confined to the United States; one is endemic in Chile and two in Mexico. Ten of the species or varieties occur in the southwestern United States and Mexico and three of these, *P. ternifolia, P. ovata* and *P. sagittata,* are distributed along the Cordillera to Argentina. The Cordilleran distribution pattern is similar to other ferns as *Notholaena sinuata*, the *N. nivea-incana* group, the *Cheilanthes pyramidalis-marginata* group and to the Umbellifers *Osmorhiza mexicana* and *Sanicula liberta.* The most extensive distribution among the pellaeas is that of *P. ternifolia* in the western highlands of the Americas from Texas to Argentina, in the Sierra de la Ventana in eastern Argentina, and it is reported by C. H. Hicken[1] from Minas Geraes although I have seen no specimens from Brazil. Both *P. ternifolia* and *P. ovata* occur in Hispaniola but the former is unique in the group in its occurrence in the Hawaiian Islands as well. The Cordilleran-Hawaiian distribution is also common to *Asplenium monanthes.* The genus occurs in Africa but within this section only the Chilian *P. myrtillifolia* and Californian *P. andromedaefolia* have a close relationship with *P. rufa* of the south African Karroo.[2] Floristic relationships between California, Chile and South Africa occur in other genera as *Acaena* in Rosaceae and *Menodora* in Oleaceae.

The southwestern United States and adjacent Mexico is the most probable center of dispersal of these species, for the ranges of all but *P. Breweri* and *P. glabella* either converge in this region or seem to be derivatives of those that do. In two species complexes it is possible to detect the derived types by the number of spores per sporangium and in these the ranges of the ancestral members converge in this same region.

In the eastern United States the most common species is *P. atropurpurea* which ranges from Guatemala to Florida, Vermont and Colorado with two isolated stations in British Columbia and in the vicinity of Lake Athabaska in Saskatchewan. The species is reported to be a triploid and apogamous by both Manton[3] and Britton.[4]

Pellaea atropurpurea, P. glabella, P. ovata and *P. sagittata* var. *cordata* are calciphilous while *P. ternifolia* and related species are reported mainly from igneous rock. Both *P. ternifolia* var. *ternifolia* and *P. sagittata* var. *cordata* occur on the lava beds in the vicinity of Mexico City. The former grows directly on the lava while the latter occurs in crevices and pockets, where soil has accumulated, along with other calciphiles as *Ophioglossum Engelmannii* and *Selaginella Wrightii. P. ternifolia* appears to tolerate a variety of habitats and a range in altitude of 200–4000 meters. Wiggins[5] reports it and also *P. sagittata* and *P. ovata* on the dry,

[1] Soc. Argent. de Cien. Nat. 13:206. 1916.
[2] Ann. Mo. Bot. Gard. 42:101. 1955.
[3] Manton, I. Prob. Cytol. & Evol. of the Pterid. Cambridge Univ. Press. 1950.
[4] Britton, D. M., University of Maryland, Dept. of Horticulture, personal correspondence.
[5] Amer. Fern Journ. 36:1. 1946.

earthen walls of Ecuadorian towns. *P. ovata* is also an epiphyte on trees and generally has a subscandent habit with fronds nearly 1¼ m. long.

Morphology

These species are not fern-like in aspect and their leaf design is undoubtedly influenced by the arid conditions in which they grow. The spores and gametophyte have remarkable tolerance to desiccation. Herbarium specimens two to five years old bore spores which were germinated in ten days. Prothallia of *P. longimucronata* were kept air-dry for two months at temperatures ranging from 80 to 100° F. and became green when watering was resumed although no sporophytes were produced. Pickett and Manuel[6] carried on some experiments on desiccation of prothallia and sporelings of *P. atropurpurea* and *P. glabella* in which some plants were air-dry for nine and some for 18½ months. When watering was resumed some of the plants became green and continued growth. After five years Pickett[7] examined the same cultures and 5 per cent showed whole or partial recovery when satisfactory growing conditions were restored.

The rhizomes grow deep in crevices or under rocks and contain an oily substance which is still present in specimens collected some forty years ago. The rhizome has two general forms—one relatively massive, up to 1 cm. in diameter, compact or somewhat elongate, multicipital and ascendent or decumbent—the other slender, cord-like, less than ½ cm. in diameter, creeping and with buds on the older portions. The vascular system of the rhizome is not a solenostele in the strict sense but approaches a dictyostele. There may be more than one foliar gap in a section of the slender and long-creeping stems and there may be several in compact stems with short internodes.

The scales of the rhizome are mostly elongate-lanceolate or elongate-triangular with a more or less filiform and tortuous apex and entire or dentate margins. Young scales are usually concolorous. Mature scales may be concolorous or bicolorous with a central dark, sclerotic stripe or basal portion. In a few species scales of the older portions of the rhizome are wholly sclerotic, brown and lustrous except for a narrow, clear border. Cells of the scale base are usually small, squarish or irregular and above they are usually 20 or more times longer than broad. Bands of constricted cells are frequent in *P. glabella* and seem to occur where the scales are appressed. Scales of the stipe base are generally similar to those of the rhizome although in *P. sagittata* the stipe and bud scales are exceptionally broad and pseudopeltate.

The plants are generally stiff and erect in habit and the fronds are coriaceous in texture. The smallest mature plants have pinnate fronds 1 cm. long and the largest are quadripinnate, up to 125 cm. long, and may be subscandent. The leaves are usually monomorphic although several species have the segments of the fertile fronds somewhat contracted. This latter condition is especially evident in

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[6] Bull. Torr. Bot. Club 53:1–5. 1926.
[7] Amer. Fern Journ. 21:49–56. 1931.

P. atropurpurea. The blade is usually elongate-triangular but is linear in *P. Breweri* and *P. ternifolia.* The blade of *P. ovata* is most elaborate with many divisions and strongly flexuous axes. In the series of species from *P. ternifolia* to *P. mucronata* a relationship exists in the pinna between the relative position of the terminal segment and the lateral segments adjacent to the rachis. The pinna has a simple, ternate form in *P. ternifolia*, is longer and has more segments in *P. longimucronata* and still more complex in *P. mucronata.* In each of these species, irrespective of the development of the pinnae, the lateral segments nearest the rachis are inclined toward the terminal segment. *P. mucronata* having the most complex pinna-form also occupies a peripheral position in the geographic range of the series and it seems possible that this is a derived form in which the blade has been elaborated.

The form and indument of the bud and the type of vernation are distinctive in some of the species. *P. atropurpurea* has lanate buds which are elongate and become uncoiled soon after they arise from the rhizome. The buds of *P. glabella* var. *glabella* are round, tightly coiled, sparsely pubescent and slowly uncoil. The stipe may be plane or sulcate on the upper surface or it may be terete. Stipe color is castaneous to black or straw colored to ruddy brown. A few species have stipes essentially light colored with dark patches. In transverse section the stipe has a single vascular bundle having the form of a flattened or sharp angled V with inrolled ends. In *P. Breweri* and *P. glabella* the fronds articulate at the stipe base. The blade is imparipinnate but not entirely so in *P. Breweri* and some specimens of *P. glabella.*

The manner in which the pinnae depart from the rachis is a useful character in distinguishing *P. atropurpurea* and *P. glabella.* In the former the pinna-rachises depart abruptly from the rachis and form broad angles while in the latter they are somewhat decurrent or adnate to the rachis below the axis and form smaller, acute angles with the rachis. The length of the pinna-rachises ranges mostly between 5 and 10 cm. but this may be up to 15 cm. in *P. ovata* and *P. andromedaefolia* or in some species it is lacking.

Venation is pinnate, free, rarely anastomosing and is usually obscure being sunk in the mesophyll. The sunken stomates give a punctate texture to the lower surface of the segments. The receptacle occupies the vein end usually less than 1/5 of the distance to the midvein and is clavate or cuneate in form. If the sporangia are abundant the sori are superficially coalescent but the vein ends are free or rarely two are fused.

The indusium is formed by the reflexed margin of the segment which may be only slightly or strongly inrolled. The tissue which functions as the indusium is usually membranaceous but may be essentially unmodified.

The sporangia stalks are as long or longer than the capsules except in *P. Pringlei* and *P. brachyptera* where they are short. The annulus is vertical, amber colored or rarely yellow and does not extend to the insertion of the stalk. In some apogamous species the annulus may be oblique or rarely a cluster of cells at the capsule apex.

Simple capitate trichomes occur in *P. brachyptera* and *P. mucronata* and occasionally in *P. longimucronata* and *P. ternifolia* var. *Wrightiana.* They are found among the sporangia and secrete a whitish yellow substance. In an old paper the chemical nature of an apparently similar substance in *Pityrogramma triangularis* is noted by Blasdale[8] in relation to the material found in *Notholaena, Cheilanthes* and *Primula.* In *Pityrogramma triangularis* the substance is called Ceroptene and consists of yellow, triclinic crystals and whitish amorphous bodies melting at 135° C. and soluble in both alcohol and xylol.

Spore color in the species with dark stipes is tan to brownish and the rugae are scarcely prominent with the exception of *P. atropurpurea.* The latter, along with the light stiped species, has prominently ornamented spores which are generally light yellow. The spores are of special interest in this group for those of apogamous strains are larger, usually monolete with 32 per sporangium in contrast to the smaller, usually trilete 64 spored non-apogamous strains. The spores remain viable for a few years; thus it is possible to germinate them and check the gametophyte state of recent herbarium specimens. A positive indication of apogamy is shown by prothallia on which sporophytes are formed subsequent to the production of antheridia although no archegonia are formed.

Cytology

The chromosome counts in this work may be regarded as preliminary until additional material is available to support them. The cytology, however, has been helpful in indicating some of the mechanisms by which these ferns reproduce and has facilitated the taxonomic disposition of several entities. In a survey of the chromosome numbers of ferns of eastern North America, Dr. Donald M. Britton[9] of the University of Maryland treated *P. glabella* var. *glabella* and he kindly agreed to do additional counts on related species of *Pellaea.* He has studied ten members of six species from aceto-carmine squashes of the spore mother cells and these are reported in the treatment of the species. The chromosome base number of $n = 29$ has been established and both triploids and tetraploids have been formed on this base. From their morphology the triploids *P. atropurpurea* and *P. sagittata* var. *sagittata* appear to be allopolyploids. *P. ternifolia* has both diploid and polyploid strains and it is possible that the latter may be a parent in the triploid *P. atropurpurea.*

Phylogeny

Since polyploidy is prevalent in the group it is difficult to plot relationships until chromosome counts are reported for all species. There is likewise difficulty in the establishment of primitive and advanced characters. A sequence of genera based on the receptacular condition within the tribe Cheilantheae is discussed by R. M. Tryon[10] in his treatment of *Doryopteris.* He regards this genus as most advanced and derived from either a Cheilanthoid or Pellaeoid stock and *Pellaea* as

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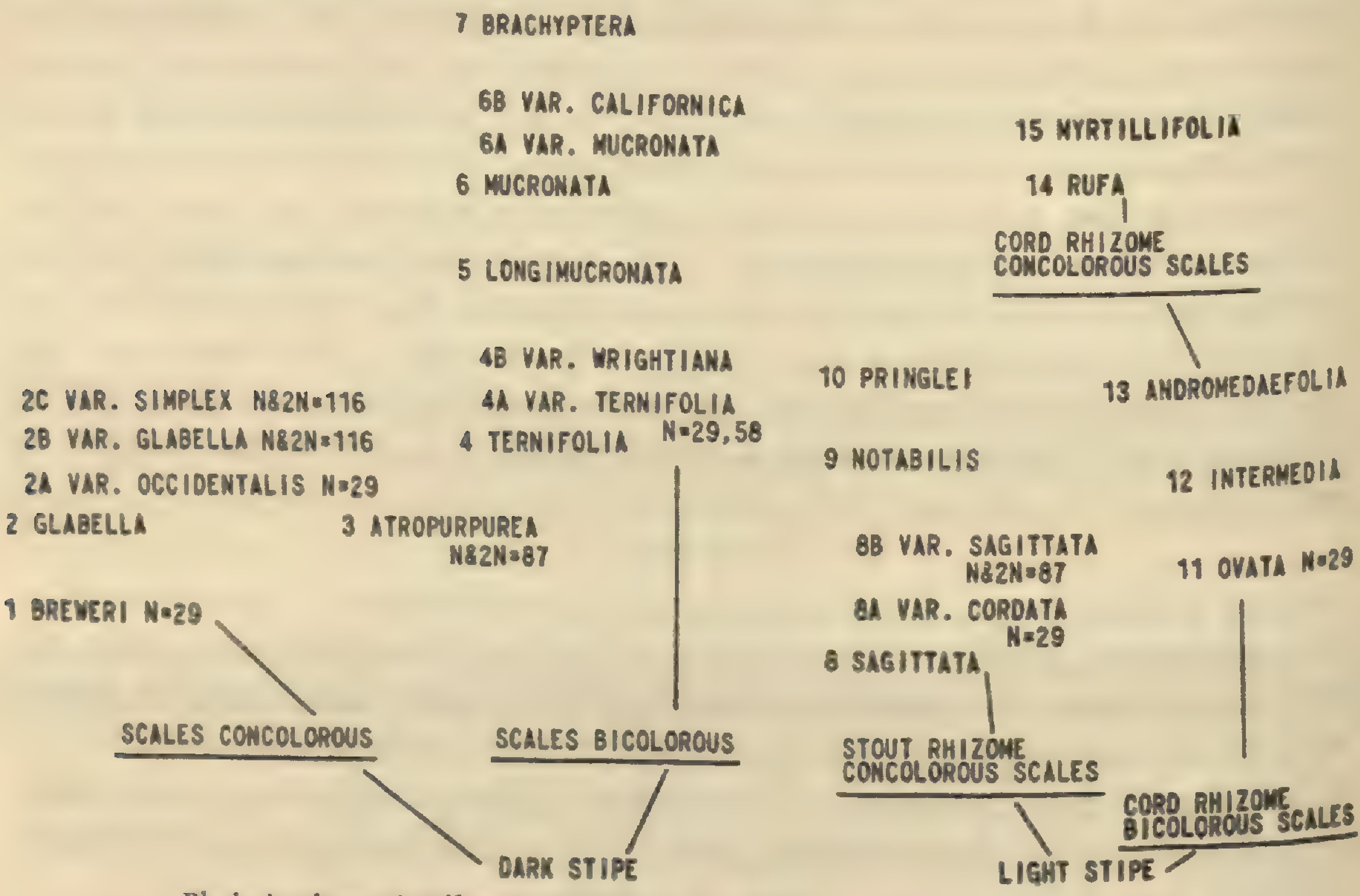
[8] Erythea 1:252. 1892.
[9] Amer. Journ. Bot. 40:575–583. 1953.
[10] Contrib. Gray Herb. No. 143. 1942.

parallel to or derived from *Cheilanthes* or *Notholaena* and perhaps intermediate to these and *Doryopteris*.

Within the section PELLAEA several natural lines are apparent. Two of these are distinguished on the basis of the color of the stipes. Dark colored stipes are considered advanced since some of the light striped species have less specialized, creeping rhizomes. Within the dark stiped group there are two distinct lines. One line composed of *P. Breweri* and *P. glabella* has evidently emerged from a Cheilanthoid stock as shown in the decurrent pinnae and the pinnate-pinnatifid division of the blade. The other line of dark stiped species is the most closely related group of the section. It appears to have evolved from *P. ternifolia* and is of such continuity that some difficulty is encountered in delimiting the species. These seem to have evolved through morphological and ecological adaptations such as those discussed by Mason[11] in his paper on the role of plant geography in taxonomy in reference to the tribe Helenieae in the southwestern United States. The lack of distinctive characters in these Compositae is interpreted as an indication of relatively recent elaboration. Among the species of *Pellaea* with light stipes those with cord-like rhizomes are considered more primitive and of these *P. ovata* is most specialized by its elaborate frond. Of the light stiped species having stout, multicipital rhizomes *P. sagittata* is regarded more specialized by its dimorphic scales. *P. notabilis* seems to be intermediate between the two main groups for although the stipes are essentially light colored their bases are dark. It is most closely related to *P. atropurpurea* on several characters.



Phyletic chart of *Pellaea* section PELLAEA with known chromosome numbers.

[11] Chronica Botanica 14:154–159. 1953.

The phyletic chart shows the relationships discussed above and the chromosome counts that have been reported.

Background of the Study

From Linnaeus to Desvaux's 'Prodrome' of 1827, six of the entities included here were placed in *Pteris*, one of the major fern genera of earlier botanical works. As interest in ferns increased the botanical gardens of Europe developed their living collections which included many from the American continents and fern classification advanced. This group was recognized as a natural genus twice within the year 1841 and thus the nomenclature has been confused from the beginning. Link[12] proposed *Pellaea* from the collections at the Berlin Gardens and John Smith[13] applied the name *Platyloma* for the same group from the collections at Kew Gardens. Smith's name, published in August, appears to have preceded that of Link. Alston has noted in the British Museum's copy of Link's work that it was issued between September 3 and 10, fide—Aag. Bibl. f. Deutsch. Lib. No. 37 p. 421. 1841. A committee on nomenclature for Pteridophytes[14] reported a unanimous vote to conserve *Pellaea* and Dr. Pichi-Sermolli,[15] Secretary of the Committee, has reviewed the matter. The International Code adopted by the 8th Congress at Paris, 1954, includes *Pellaea* among the genera to be conserved.

Presl[16] took up a still earlier name, *Allosorus* of Bernhardi and treated these species in section MONOMORPHI along with species now referred to *Jamesonia, Doryopteris* and *Cheilanthes*. Otto Kuntze[17] follows Presl in order to avoid conflict with *Pellia* of Raddi and *Pella* of Gaertner and since he believed Presl's work more adequate than Link's.

Fée[18] distributed these species among four of six groups, based largely on the shape of the blade, he includes in *Pellaea*.

W. J. Hooker[19] also considered vegetative characters as diagnostic for he arranged these species in *Pellaea* according to the division of the blade. His diagnosis of the species, illustrations and general information on the collections he examined are better than previous accounts.

Prantl[20] proposed the section EUPELLAEA for these species as one of eight sections and indicated that these are the *Pellaea* of Link. He considered the condition of the blade, the sori, the vascular system and scales. Diels[21] essentially followed Prantl's scheme.

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[12] Fil. Sp. Hort. Bot. Berol. Cult. 59. 1841.
[13] Journ. Bot. ed. W. J. Hooker 4:160. 1841.
[14] Taxon 3:70. 1954.
[15] Webbia 9:428. 1953.
[16] Tent. Pterid. 151. 1836.
[17] Rev. Gen. Pl. 2:802. 1891.
[18] Gen. Fil. 128. 1850–52.
[19] Sp. Fil. 2:130–153. 1885.
[20] Engl. Bot. Jahrb. 3:415. 1882.
[21] Engl. & Prantl, Nat. Pflanzenfam. 1^4:266. 1899.

Until studies of the African pellaeas and other genera of the Cheilantheae are completed the disposition of this group as a section of *Pellaea* seems the most practicable course.

Use and Cultivation

These neat, novel plants were popular in English stoves and American conservatories during the Victorian era. Two of the plants were introduced for greenhouses by Messrs. Veitch & Sons of Chelsea who obtained them from California. They were described as species and the types at Kew are nursery specimens more robust than the native Californian plants. *P. brachyptera, P. ovata, P. andromedaefolia* and *P. mucronata* were included in the florist trade of the period and the last is described as a handsome house plant producing as many as 75 fronds. Many of the species are now grown in botanical collections for they are easily cultivated. W. J. Hooker noted that several of the pellaeas were cultivated in the temperate fern houses at Kew more than a hundred years ago and at present the hanging baskets of *P. ovata* and *P. sagittata* in these fern houses are most attractive. Several of the Mexican pellaeas are grown in the University of California greenhouses and *P. ternifolia* var. *ternifolia* was volunteering there in pots of cacti and succulents. Seven species have been grown in the experimental greenhouse at the Missouri Botanical Garden. The plants require little special care other than a rock substrate and good drainage. *P. atropurpurea,* an attractive rock garden plant, is evergreen and does especially well on native limestone.

There are a few references on the medicinal uses of *Pellaea*. *P. mucronata* is reported to make a palatable beverage recommended for the kidneys and as a blood purifier. The vernacular name *Tea Fern* and the Tejon Indian name *Calagula* have been applied. Chilian miners use the name *Coca* or *Yerba Coca* for the local *P. myrtillifolia* and prepare an infusion of it taken to allay pain.

Acknowledgements

I am indebted to the curators of the herbaria of the following institutions for the generous loan of specimens: Chicago Natural History Museum, Gray Herbarium, Muséum National d'Histoire Naturelle, Paris, Naturhistoriska Riksmuseum, Stockholm, Naturhistoriska Riksmuseum Paleobotanical Department, Stockholm, New York Botanical Garden, United States National Museum, University of British Columbia, University of California, Cornell University, University of Kansas, University of Michigan, University of Minnesota, University of Utah, State College of Washington, Pullman, University of Washington, Seattle, University of Wyoming and Yale University. The abbreviations for these and other herbaria are taken from 'Index Herbariorum,' part I (Regnum Vegetabile vol. 2) compiled by Lanjouw and Stafleu.

I wish to thank Mr. F. Ballard of Kew, Mr. J. A. Crabbe of the British Museum, Mme. Tardieu-Blot of Paris, and Mr. C. V. Morton of the United States National Herbarium for courtesies extended during the course of this study. Prof. Maximino Martínez of the Herbario Nacional del Instituto de Biologia, Universidad Nacional

de Mexico, gave kind assistance on Mexican localities, and Prof. Efraim Hernández-Xolocotzi of the Escuela Nacional de Agricultura, Chapingo, was of much help and good company in collecting Mexican pellaeas.

I am especially grateful for collections of living plants which were received from Dr. E. F. Castetter of the University of New Mexico, Dr. Seville Flowers of the University of Utah, Dr. G. B. Ownbey of the University of Minnesota and Mr. J. W. Thompson of Seattle.

Dr. Donald M. Britton of the University of Maryland has done the chromosome studies which are reported in this treatment. The information has been incorporated in the taxonomy and phylogeny of the group. A more detailed account of the cytology and evolution of these ferns is in preparation by Dr. Britton and myself.

I am indebted to Mrs. Bernadette Velick who has helped me in the preparation of the drawings.

For his patient council and kindly criticism I am most grateful to my husband, Rolla M. Tryon, under whose guidance this study has been made.

Synopsis

Pellaea Link, Fil. Sp. Hort. Bot. Berol. 59. 1841, nom. conserv. Section pellaea.

Eupellaea Prantl, Engl. Bot. Jahrb. 3:415. 1882.

The natural characters of the group are best expressed in the imparipinnate, usually coriaceous blade; continuous marginal indusium; terminal sori on discrete and usually clavate vein ends; stipe and rachis tan to black, usually glabrous, smooth, without wings or conspicuous scale scars; costa of the segments mostly obscure; sporangia usually long stalked; spores yellowish tan to brown, smooth or rugose.

Although the section is not defined by a few striking characteristics it is a relatively homogeneous one. Among the species listed below some may not conform in all respects but are most properly placed here on the sum of their characters.

Type species: *Pellaea atropurpurea* (L.) Link.

Species: 1. *P. Breweri* D. C. Eaton, 2. *P. glabella* Mett. ex Kuhn, 2A. var. *occidentalis* (E. Nelson) Butters, 2B. var. glabella, 2C. var. *simplex* Butters, 3. *P. atropurpurea* (L.) Link, 4. *P. ternifolia* (Cav.) Link, 4A. var. ternifolia, 4B. var. Wrightiana (Hook.) A. F. Tryon, 5. *P. longimucronata* Hooker, 6. *P. mucronata* (D.C. Eaton) D. C. Eaton, 6A. var. mucronata, 6B. var. *californica* (Lemmon) Munz & Johnston, 7. *P. brachyptera* (Moore) Baker, 8. *P. sagittata* (Cav.) Link, 8A. var. cordata (Cav.) A. F. Tryon, 8B. var. sagittata, 9. *P. notabilis* Maxon, 10. *P. Pringlei* Davenp., 11. *P. ovata* (Desv.) Weatherby, 12. *P. intermedia* Mett. ex Kuhn, 13. *P. andromedaefolia* (Kaulf.) Fée, 14. *P. rufa* A. F. Tryon, 15. *P. myrtillifolia* Mett. ex Kuhn.

The position of *Pellaea Bridgesii* Hook., which in its general aspect resembles some of the species treated here and occurs mainly in California, remains a problem. I have excluded it on the basis of the conduplicate segments lacking reflexed margins, the short stalked sporangia which are borne on an elongated receptacle one quarter to one half the distance to the costa and which persist in a cup-like

form after dehiscence. It resembles some species of *Notholaena* in the length of the receptacle and in the abundant waxy indument produced among the sporangia.

KEY TO SPECIES

a. Stipe and rachis castaneous to black; spores usually with a sparsely rugose exospore. b.

b. Scales of the rhizome concolorous; stipe and rachis terete or elliptical. c.

c. Fronds monomorphic; pinnae sessile or the stalks somewhat decurrent on the rachis and arising at acute angles to the rachis; stipe and rachis glabrous or sparsely pubescent; scales of the rhizome discrete, a uniform rust-brown color. d.

d. Rhizome massive with numerous compressed, short, articulated stipe bases; mature fronds with rachises mostly green in the terminal portion of the blade, the apical segments strongly decurrent; the basal pinnae without persistent stalks often sessile or subsessile.........1. *P. Breweri*, p. 135

d. Rhizome moderately stout with few stipes persistent, these more or less spreading; mature fronds with rachises mostly brownish in the terminal portion of the blade, the apical segments somewhat decurrent or stalked; the basal pinnae with persistent stalks.........2. *P. glabella*, p. 138

c. Fronds dimorphic; pinnae stalked, not decurrent and arising at broad angles to the rachis; stipe and rachis scurfy with appressed pubescence; scales of the rhizome matted, rust colored with the young tips light tan.........3. *P. atropurpurea*, p. 144

b. Scales of the rhizome bicolorous with a sclerotic central stripe or base; stipe and rachis sulcate, convex or plane on the upper surface. e.

e. Segments with opaque whitish borders, usually membranaceous; sporangia long stalked. Oklahoma to Utah southward to Argentina, Dominican Republic, Hawaiian Islands. f.

f. Basal pinnae usually less than twice as long as broad, entire or divided into 3–11 segments; the pinnae-rachises up to 2 cm. long.........4. *P. ternifolia*, p. 149

f. Basal pinnae usually more than twice as long as broad, divided into 9–21 segments; the pinna-rachises up to 7 cm. long.........5. *P. longimucronata*, p. 155

e. Segments entirely green, the border undifferentiated or narrow, lutescent green; sporangia short stalked. Southern Oregon, California, Baja California. g.

g. Ultimate segments of the basal pinnae shorter than the pinna-rachis; blade ovate-triangular to rhomboid; pinnae ovate-linear.........6. *P. mucronata*, p. 157

g. Ultimate segments of the basal pinnae longer than the pinna-rachis; blade linear; pinnae semi-circular.........7. *P. brachyptera*, p. 162

a. Stipe and rachis straw colored to ruddy brown or darker at the base and mottled above; spores usually with a prominent rugose exospore. h.

h. Rhizome moderately stout, compact; scales of the stipe base and buds tawny, broad, cordate or pseudo-peltate; fronds approximate; spores sparsely rugose. .... 8. *P. sagittata*, p. 164

h. Rhizome usually slender, cord-like and creeping, or moderately stout and compact; scales of the stipe base and buds tan, rust colored or brown, slender, acicular to lanceolate-triangular; fronds distant or approximate; spores prominently rugose. i.

i. Blades usually once or twice pinnate; pinnae with 1–3 segments; segments elongate-lanceolate or lobed (stellate to ternate). j.

j. Veins, except for the midvein, obscure; pinnae elongate-lanceolate, several times longer than broad, subcoriaceous. Nuevo León and Tamaulipas. .... 9. *P. notabilis*, p. 170

j. Veins evident; pinnae stellate to ternate, nearly as long as broad, chartaceous or herbaceous. Central and western Mexico. .... 10. *P. Pringlei*, p. 172

i. Blades tri–quadripinnate or more highly divided; pinnae generally with 10–50 segments; segments mainly ovate. k.

k. Rachis and pinna-rachises strongly flexuous. .... 11. *P. ovata*, p. 174

k. Rachis and pinna-rachises straight. l.

l. Mature rhizome scales bicolorous. Southwestern United States and Mexico. m.

m. Veins obscure; segments coriaceous; buds pubescent. Texas, New Mexico, Arizona and northern Mexico. .... 12. *P. intermedia*, p. 177

m. Veins visible on the lower surface of the segments; segments herbaceous; buds paleaceous. California. .... 13. *P. andromedaefolia*, p. 179

l. Mature rhizome scales concolorous. Chile, South Africa.

n. Rhizome cord-like, long-creeping; spores essentially smooth. South Africa. .... 14. *P. rufa*, p. 184

n. Rhizome moderately stout, compact; spores rugose. Chile. .... 15. *P. myrtillifolia*, p. 184

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1. Pellaea Breweri D.C. Eaton, in Proc. Amer. Acad. 6:555. 1865. (Lectotype: *Brewer 2038* YU!, Isotypes: MO! NY!, Paratypes: *Brewer 1919, 2102* YU!, Photo of Holotype and Paratypes: GH! US! Fig. 1. Map 1.

Allosorus Breweri (D.C. Eaton) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome compact, ascendent, massive with many compressed bases of articulated stipes. Scales of the rhizome entangled or matted, uniform rust brown, these and those of the base of the stipes concolorous, lustrous, acicular, flexuous, the margins sinuate, not dentate, the cells of the scale base short, rectangular or with oblique end walls, the apex attenuate. Fronds 2.5–21.0 cm. long, bent

or arcuate, monomorphic, the buds with sparse, reddish brown pubescence. Stipe and rachis terete, often flat when dry, sparsely pubescent, castaneous, lustrous, becoming darker and dull with age, the stipe with prominent lines of articulation, readily breaking at right angles to the axis, the rachis green at the apex. Blade 1.5 cm. long and 0.5 cm. broad to 16.0 cm. long and 3.5 cm. broad, linear-oblong, once pinnate or pinnate-pinnatifid, pure green, subglaucous, the pinnae of nearly the same length, departing at acute angles to the rachis, the upper pinnae entire, sessile, usually strongly decurrent on the rachis, the lower pinnae deeply 2-lobed, unilateral or mitten-shaped, rarely 3-lobed, subsessile or with short, green, rarely brown stalks, decurrent, the axils usually green, without pinna-rachises. Segments 0.5 cm. long and 0.3 cm. broad to 2.5 cm. long and 1.0 cm. broad, linear-ovate to deltoid, usually lobed, herbaceous, the border narrow, whitish, crenulate, the apex muticous. Sporangia sessile or subsessile, the annulus pale yellow, rarely amber colored. Spores 64 per sporangium, tetrahedral-globose, dark to light brown, with a scarcely prominent rugose exospore.

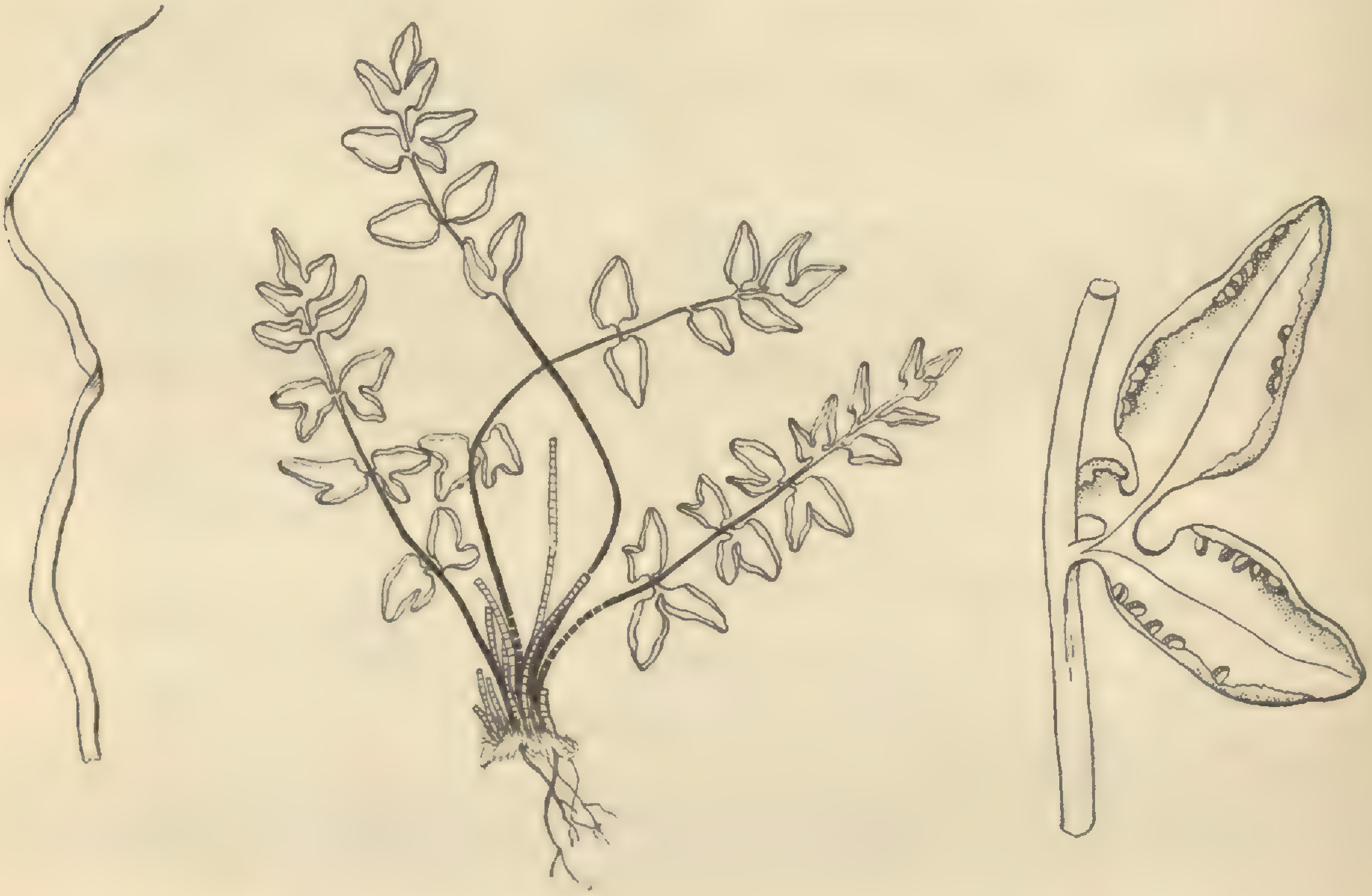
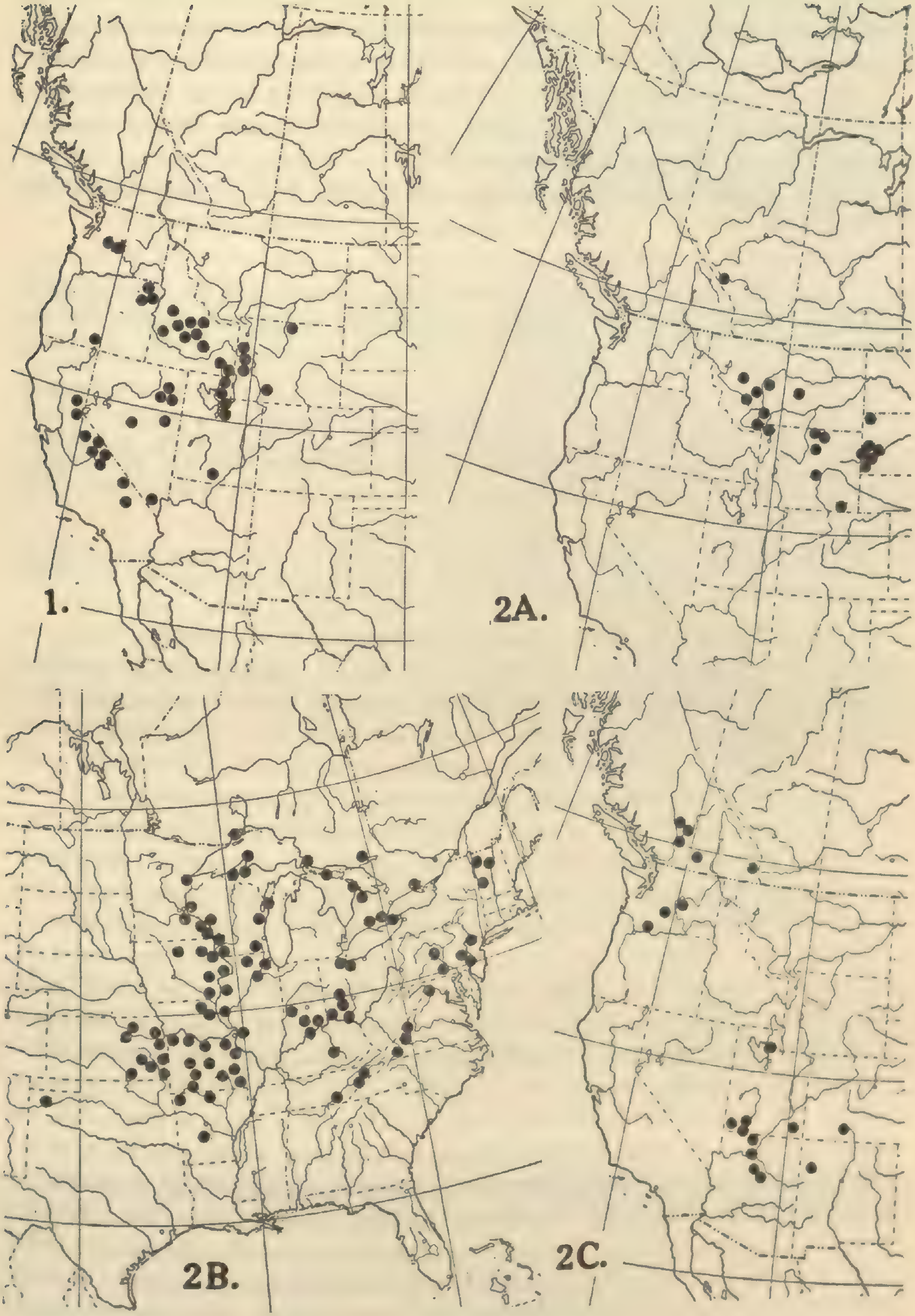


Fig. 1. *Pellaea Breweri*, plant × ½; pinna; rhizome scale.

P. Breweri resembles *P. glabella* more than any other member of the genus and a relationship exists here between *Pellaea* and several Mexican and South American species of *Cheilanthes*. In *P. Breweri* and *P. glabella* the division and lobing of the frond, the position and attachment of the pinnae on the rachis and the articulation of the stipes are more like those of *Cheilanthes Brandegii*, *C. allosuroides*, *C. pyramidalis* and *C. marginata* than other pellaeas.

The mature fronds of *P. Breweri* articulate at constricted bands on the stipe. No special tissue is developed in the stipe but the hypodermis and cortex are com-



1. **Distribution of *Pellaea Breweri*.**

2A. Distribution of *Pellaea glabella* var. *occidentalis*, 2B. var. *glabella*, 2C. var. *simplex*

posed of relatively large, thin-walled cells. Fractures occur from the center of the stipe outward, possibly due to the mechanical strain set up by the drying of the delicate central tissue. This is also evident in *P. glabella*, particularly var. *occidentalis*.

The chromosome number reported by Dr. D. M. Britton is n = 29 from specimens collected by Seville Flowers, Salt Lake County, Utah, Big Cottonwood Canyon, Wasatch Mountains, on July 25, 1953.

Usually on granite rocks or basalt but also reported from limestone, at 1600–3800 m.

Representative specimens:

United States. wyoming: *M. & R. P. Ownbey 1878* (GH, MO, NY, WS); *Williams & Pierson 834* (GH, MO, US). idaho: *Hitchcock & Mulick 11004* (NY, US, WS, WTU); *Thompson 14022* (GH, MO, US, WTU). utah: July 25, 1953, S. *Flowers* (MO); *Goodding 1114* (MO, US); *Maguire et al. 13153* (GH, MO, US, WS). nevada: *Clokey 7815* (MO, US, UT, WS, WTU); S. *Watson 1361* (GH, US, YU). washington: *Thompson 7832* (US), *9515* (GH, NY, MO, US, WS, WTU). oregon: *Coville & Leiberg 301* (US); *Thompson 13220* (GH, NY, MO, US, WS, WTU) california: *Alexander & Kellogg 3103* (MO, US, WS); *Bolander 6243* (GH, MO, US, YU); Among rocks at Ebbetts Pass, Aug. 4–16, 1863, *Brewer 2038, 2102* (NY, YU); *Duran 2811* (GH, MO, NY, US, WTU).

2. Pellaea glabella Mett. ex Kuhn, in Linnaea 36:87. 1869. (Lectotype: Specimen cited from Kimmswick, near St. Louis, Mo. B?).

Rhizome moderately stout, compact, decumbent or ascendent, multicipital. Scales of the rhizome discrete and usually not matted, uniform rust brown, these and those at the base of the stipes concolorous, lustrous, linear, flexuous, often with horizontal bands of constricted cells, the margins sinuous or with broad irregular teeth, the cells of the scale base small, squarish, or elongate with oblique end walls, the apex somewhat attenuate, more or less tortuous, discrete, not entangled. Fronds 1–36 cm. long, usually lax, arcuate or sinuous, monomorphic, the buds sparsely pubescent. Stipe and rachis terete, glabrous or nearly so, castaneous, lustrous, becoming darker and dull with age, the stipe breaking at right angles to the axis, occasionally with perpendicular lines of articulation, the rachis castaneous or greenish at the apex. Blade 0.75 cm. long and 0.5 cm. broad to 21 cm. long and 8 cm. broad, linear or ovate-lanceolate, once to twice pinnate, clear or bluish green, glaucous or subglaucous, the lower pinnae less than twice as long as the upper, departing at acute angles to the rachis, the upper pinnae entire or auriculate, sessile or subsessile, the lower pinnae entire, 2–5 lobed or once pinnate with 3–7 segments, stalked, the pinna-stalks somewhat decurrent, the axils colored as the rachis, the pinna-rachises up to 5 cm. long. Segments 0.5 cm. long and 0.3 cm. broad to 3.5 cm. long and 1.0 cm. broad, oblong to linear-ovate, usually lobed or auriculate, herbaceous to subcoriaceous, the border narrow, whitish, crenulate, the apex muticous to submucronate. Sporangia with long or short stalks, the annulus amber colored, occasionally oblique. Spores 32 or 64 per sporangium ellipsoidal or tetrahedral-globose, occasionally dumbbell-shaped, rusty brown, the exospore sparsely to moderately rugose.

In his studies of *P. glabella*, Butters segregated two western species on the

basis of differences in frond size, shape of the pinnae and vascular bundle and the size of the spores.[22] The size and number of spores per sporangium are of interest here for they reflect cytological differences. Britton[23] reports the chromosome number of *P. glabella* var. *glabella* from southern Ontario as n = 116 and considers this to be a tetraploid on the base number of 29. The plants are apogamous and the sporangia are 32 spored. He reports a tentative count of *P. glabella* var. *simplex*, collected by *J. W. Thompson 17246* from Grant Co., Washington, as also n = 116 and the material is 32 spored and apogamous. The monoploid number predicted in the above counts is realized in *P. glabella* var. *occidentalis*. Specimens collected by *G. B. & F. Ownbey 1676* from Laramie Hills, Albany Co., Wyoming, have 64 spored sporangia, a normal sexual development and the chromosome count was determined as n = 29. Thus the 116 numbered members may be considered as tetraploids derived, at least in part, from *P. glabella* var. *occidentalis*.

On rocks or cliffs, in crevices, usually on limestone, rarely on granitic rocks.

Arizona north to southern British Columbia and northeast across the United States to Vermont.

Key to Varieties

Spores 64 per sporangium; fronds 1–15 cm. long, once pinnate, the pinnae with 2 or 3 lobes, usually sessile or with stalk and rachis up to 0.2 cm. long. Alberta to Wyoming and South Dakota. 2A. var. *occidentalis*, p. 139

Spores 32 per sporangium; fronds 1–36 cm. long, once to twice pinnate, the pinnae deeply lobed or with 3–7 segments, with stalk and rachis up to 5.0 cm. long.

- Fronds 4–36 cm. long, the basal pinnae persistent, with stalk and rachis up to 5.0 cm. long. Vermont to Minnesota and Texas. .... 2B. var. *glabella*, p. 141
- Fronds 1–20 cm. long, the basal pinnae usually withered, with stalk and rachis up to 1.0 cm. long. British Columbia to Washington and Utah to New Mexico. .... 2C. var. *simplex*, p. 142

2A. Pellaea glabella var. occidentalis (E. Nelson) Butters, in Amer. Fern Journ. 7:82. 1917. Fig. 2A. Map 2A.

Pellaea atropurpurea var. *occidentalis* E. Nelson, in Fern Bull. 7:30. 1899. (Holotype: *A. Nelson 1919*! RM!, Isotype: MO! NY!).
Pellaea pumila Rydb. in Mem. N. Y. Bot. Gard. 1:4. 1900. (Holotype: *Rydberg 1101* NY!, Isotype: US!).
Pellaea occidentalis (E. Nelson) Rydb. loc. cit. 466. 1900.

Rhizome slender, somewhat ascendent. Scales of the rhizome and base of the stipes sinuate or the margins with few blunt teeth or erose, the cells of the base of the scales squarish. Fronds 1–15 cm. long. Stipe usually with perpendicular lines of articulation. Blade 0.75 cm. long and 0.5 cm. broad to 10 cm. long and 4 cm. broad, once pinnate or pinnate-pinnatifid, bluish green. Segments ovate to oblong,

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[22] Amer. Fern Journ. 7:77. 1917; 11:39, 75. 1921.
[23] Amer. Journ. Bot. 40:575. 1953.

mostly entire or 2- or 3-lobed and mitten-shaped, those of the basal pinnae withering early with persistent petiolules, the apex muticuous, rarely submucronate. Sporangia stalks equal to the capsule length. Spores 64 per sporangium, mostly tetrahedral-globose, the exospore with short, moderately prominent rugae.

Generally these are smaller plants than the others of the *P. glabella* group but not conspicuous in any unique structure. Within the geographic range of the species they occupy a central position, mostly discrete and more restricted than the other varieties. As mentioned in the discussion of *P. atropurpurea* the possibility exists that hybrids were produced between that species and *P. glabella* var. *occidentalis* producing the eastern var. *glabella* and the western var. *simplex*. The ranges of *P. atropurpurea* and var. *occidentalis* are contiguous in the Black Hills of South Dakota and nearly so in the vicinity of Banff, Alberta. A few specimens from the former region appear intermediate. *P. glabella* var. *occidentalis* is undoubtedly the source from which the polyploid members of the complex have been derived either through hybridization or possibly autopolyploidy.

In narrow fissures of limestone ledges at 1300–2800 m.

Banff, Alberta, southeast in the United States to Wyoming and the Black Hills of South Dakota.

Representative specimens:

Canada. alberta: Aug. 14, 1920, *Butters* (US); *Ulke 901* (NY).

United States. montana: *Blankenship 638* (MO, RM, US); *Suksdorf 463* (GH, WS). wyoming: *L. C. Anderson 648* (UTC); Laramie Hills, June 13, 1896, *Aven Nelson 1919* (MO, NY, RM); *A. & E. Nelson 6837* (GH, MO, NY, US); *G. B. & F.*

Fig. 2A. *Pellaea glabella* var. *occidentalis*, plant × ½; pinna; rhizome scale.

Ownbey 1676 (MO). SOUTH DAKOTA: *Palmer 37126* (GH, MO); Bull Springs, limestone district west of Custer, Black Hills, July 27, 1892, *Rydberg 1191* (GH, NY, US).

2B. PELLAEA GLABELLA var. **glabella** Fig. 2B. Map 2B.

Pellaea atropurpurea var. *Bushii* Mack. ex Mack. & Bush, Man. Fl. Jackson Co., Mo., 5. 1902. (Holotype: *Mackenzie 447* NY!, Isotype: RM!).
Cassebeera atropurpurea var. *minima* Eggert ex Farw. in Amer. Midl. Nat. 12:281. 1931. (Holotype: *Eggert, July 1878* MICH!).
Pellaea atropurpurea var. *minima* Eggert ex Farw. loc. cit. 1931, in synon.
Cassebeera atropurpurea var. *glabella* (Mett. ex Kuhn) Farw. loc. cit. 1931.
Pellaea atropurpurea f. *glabella* (Mett. ex Kuhn) Clute, Our Ferns, 109, 386. 1938.

Rhizome moderately stout, decumbent. Scales of the rhizome and base of the stipes sinuate or the margins with irregular, broad teeth, the cells of the base of the scales mostly elongate with oblique end-walls. Fronds 4–36 cm. long. Stipe occasionally with perpendicular lines of articulation. Blade 2 cm. long and 1 cm. broad to 21 cm. long and 8 cm. broad, once to twice pinnate, bluish green. Segments oblong-lanceolate, entire or auriculate or 3–5 lobed, persistent, the apex submucronate. Sporangia stalks as long or shorter than the capsule. Spores 32 per sporangium, ellipsoidal or tetrahedral-globose, the exospore with sparse, scarcely prominent rugae.

Variety *glabella* appears to represent a genotype both vigorous and well adapted to the arid, limestone ledges which it occupies in the central and eastern United States. It is generally distinguished from the western varieties by its larger size.

Fib. 2B. *Pellaea glabella* var. *glabella*, plant × ½; pinna; rhizome scale; section of the rachis with pinna-stalks.

As indicated in the discussion of *P. atropurpurea, P. glabella* var. *glabella* is similar in several respects although the two can be distinguished by several characters as follows:

Pellaea glabella var. *glabella*	*Pellaea atropurpurea*
Leaves monomorphic.	Leaves dimorphic.
Leaves lax, arcuate or sinuous, 4–36 cm. long.	Leaves erect, straight, stiff, 6–50 cm. long.
Blades linear to elongate-ovate.	Blades elongate-triangular.
Stipe and rachis glabrous or with few bicolorous hairs.	Stipe and rachis hispid, scurfy.
Pinnae at acute angles to the rachis, somewhat decurrent, departing gradually (fig. 2B).	Pinnae at broad angles to the rachis and departing abruptly (fig. 3).
Basal pinnae with 3–7 segments; less than twice as long as the upper pinnae.	Basal pinnae with 3–15 segments; usually 2 or more times as long as the upper pinnae.
Scales of the rhizome discrete, uniformly rust-brown, lustrous, the tips not entangled.	Scales of the rhizome appressed, matted, dull tawny to rust colored, the young tips tan and entangled.
Margins of the fertile segments usually strongly reflexed with relatively few sporangia exposed.	Margins of the fertile segments plane with abundant sporangia exposed.

On limestone, calcareous sandstone or dolomite cliffs or bluffs in shaded crevices or exposed ledges at less than 400 m.

Northwestern Texas to the north shore of Lake Superior, Ontario, and east to Tennessee and Vermont.

Representative specimens:

CANADA. ONTARIO: *Soper & Burcher 2074* (GH, MO); *Taylor et al. 115* (US).

UNITED STATES: VERMONT: 1903, *Baxter* (MO); *Fellows 481* (US). PENNSYLVANIA: Aug. 1920, *Wherry & Pretz* (US). NEW JERSEY: *Mackenzie 4621* (MO). WEST VIRGINIA: Sept. 1937, *Spawn* (US). VIRGINIA: *Adams & Wherry 2257* (GH); *Wood 3644* (GH). OHIO: *Roth et al. 670* (US); *Camp 1053* (NY). KENTUCKY: Aug. 1938, *Richards* (US). TENNESSEE: *Jamison & Shaver 4161* (MO); *Underwood & Sharp 2523* (MO). MICHIGAN: *Hagenah 1157* (US); Aug. 1892, *Wheeler* (RM, US). INDIANA: *R. M. & P. F. Tryon 4348* (MO, US). ILLINOIS: *Evers et al. 671* (GH). MINNESOTA: *M. F. & J. W. Moore 13563* (MIN, MO). IOWA: *Anderson (Pl. Exsicc. Gray. 902)* (GH, MO, NY, RM, US, WS). MISSOURI: *Bush 2837* (GH, MO, NY, US); Near St. Louis, July, 1878, *Eggert* (MICH); Limestone rocks at Swope Park, Sept. 13, 1901, *Mackenzie 447* (NY, RM). ARKANSAS: May, 1923, *Buchholz* (MO, US). NEBRASKA: Nov. 1895, *Williams & Wilcox* (US). KANSAS: *Horr E463* (RM, US, UT, WS). TEXAS: *D. S. & H. B. Correll 13085* (MO).

2C. PELLAEA GLABELLA var. SIMPLEX Butters, in Amer. Fern Journ. 7:84, 1917. (Holotype: *Heacock 272* GH!, Photo: MO!, Isotypes: MO! NY!).

Fig. 2C. Map 2C.

Pellaea Suksdorfiana Butters, in Amer. Fern Journ. 11:40. 1921, based on *P. glabella* var. *simplex* Butters.

Pellaea atropurpurea var. *simplex* (Butters) Morton, in Leaf. West. Bot. 6:156. 1951.

Rhizome moderately stout, ascendent. Scales of the rhizome and base of the stipes sinuate or irregularly dentate, the cells of the base of the scales squarish or with oblique end walls. Fronds 1–20 cm. long. Stipe rarely with perpendicular lines of articulation. Blade 1.0 cm. long and 0.8 cm. broad to 14.0 cm. long and

4.5 cm. broad, usually once pinnate or pinnate-pinnatifid, or occasionally twice pinnate, clear green. Segments oblong-lanceolate, 3–5 lobed frequently with 2 or more small auricles, segments of the basal pinnae withering early with persistent petiolules, the apex muticous or submucronate. Sporangia long stalked, the annulus often oblique. Spores 32 per sporangium, ellipsoidal or tetrahedral-globose occasionally dumbbell-shaped, the exospore with sparse, scarcely prominent rugae.

Fig. 2C. *Pellaea glabella* var. *simplex*, plant × ½; pinna; rhizome scale.

The distribution of var. *simplex* is discontinuous, occurring in southern British Columbia to southern Washington and in northern Utah to central Arizona and northern New Mexico with a gap in the intervening states. In the few specimens available there is no apparent morphological differentiation between collections from the two isolated areas. In the discussion of *P. atropurpurea* it is suggested that this disrupted distribution may be due to the independent hybrid origin of *P. glabella* var. *simplex* in the two isolated regions where the ranges of *P. atropurpurea* and *P. glabella* var. *occidentalis* were contiguous.

On dry limestone or sandstone cliffs or ledges at 900–3000 m.

British Columbia, Washington, Utah, Arizona, New Mexico, Colorado.

Representative specimens:

Canada. british columbia: Carbonate Draw, Selkirk Mts., July 14, 1904, *Heacock 272* (GH, MO, NY); *Taylor & Lewis 172* (MO, Univ.B.C.); *J. W. & E. M. Thompson 362* (MO, NY, US, WS, WTU).

UNITED STATES. WASHINGTON: Cliffs along the Columbia river, Aug. 11, 1892, *Suksdorf 2038* (MO, NY, US, WTU). UTAH: *Rydberg & Garrett 9421* (NY, RM, US, UT). ARIZONA: *Collom LJC13* (US); *Tracy 267* (YU). COLORADO: *Loew*, Wheeler Exped. 1873 (YU). NEW MEXICO: 1883, *Mathews* (GH).

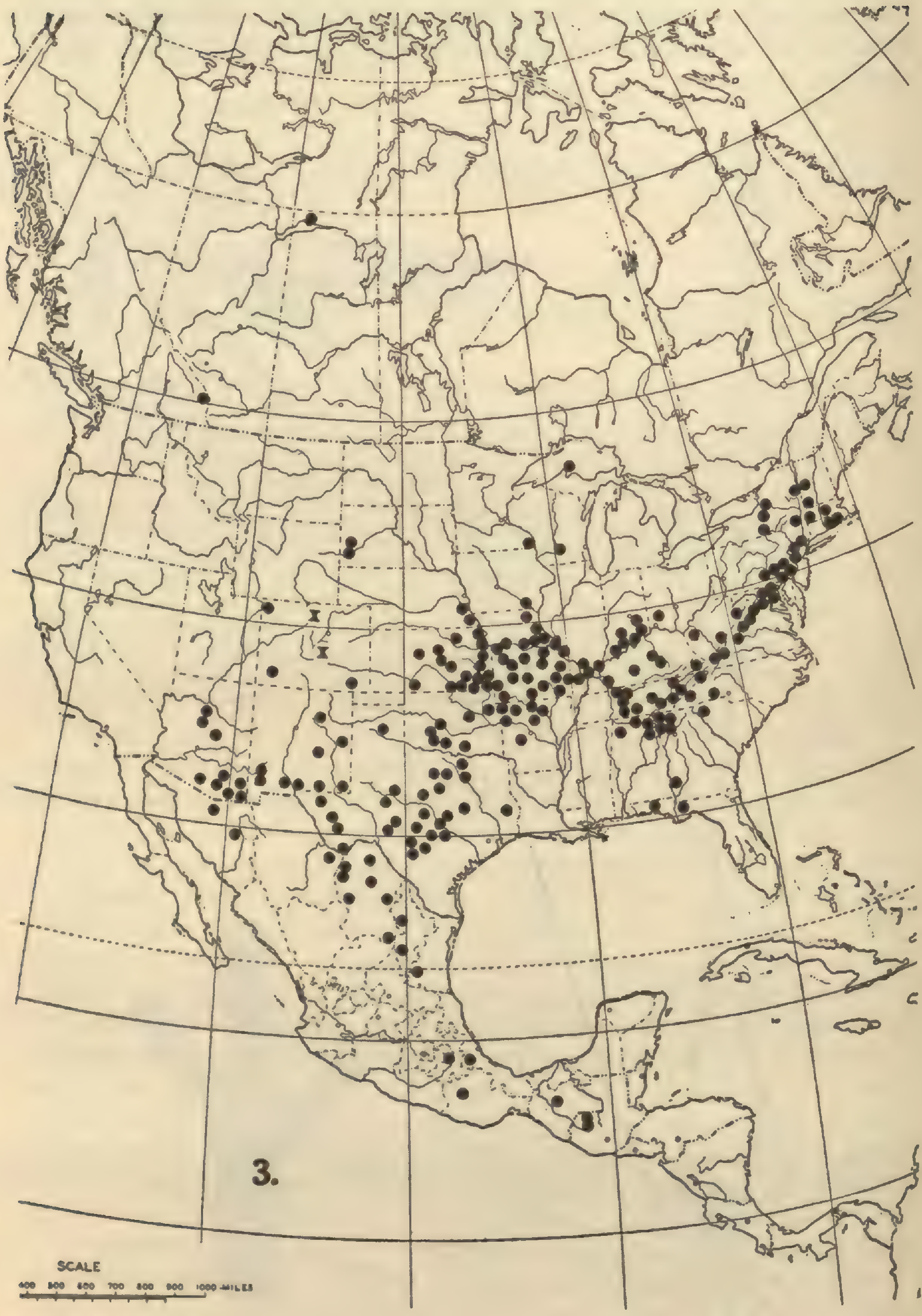
3. PELLAEA ATROPURPUREA (L.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841.
Fig. 3. Map 3.

Pteris atropurpurea L. Sp. Pl. 2:1076. 1753. (Holotype: *Clayton 682*, Point-look-out on the Rappahanock river, Va. BM). The Clayton collection was not found at the British Museum; a single frond, collected by Kalm, in the Linnean Herbarium is *P. atropurpurea.*
Pteris thalictroides Muhl. "Ind. Fil. Lancast." in Trans. Amer. Phil. Soc. 3:182. 1793, nom. nud., not *P. thalictroides* (L.) Sw. 1801.
Asplenium atropurpureum (L.) Bernh. in Schrad. Neu. Journ. 1^2:10. 1806.
Pteris spiculata Schkuhr, Krypt. Gewäch. 1:92, *t. 100.* 1809. (Lectotype: *t. 100*, loc. cit.).
Pteris atropurpurea var. *venosa* Pursh, Fl. Am. Sept. 2:668. 1814. (Holotype: *t. 101*, Schkuhr, Krypt. Gewäch.).
Pteris atropurpurea var. *punctata* Pursh, Fl. Am. Sept. 2:668. 1814. (Holotype: *t. 100*, Schkuhr, Krypt. Gewäch.). It is apparent from Schkuhr's text and figures that the table numbers are reversed in Pursh's reference to that work.
Allosorus atropurpureus (L.) Kze. ex Presl, Tent. Pterid. 153. 1836.
Platyloma atropurpurea (L.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.
Nothochlaena atropurpurea (L.) Keyserl. Polyp. Cyath. Herb. Bung. 30. 1873.
Pellaea atropurpurea var. *cristata* Trel. in Rep. Mo. Bot. Gard. 12:34. 1901. (Holotype: *Pauls*, Missouri, in 1899, MO!).
Pellaea atropurpurea var. *venosa* (Pursh) Gilb. List N. Amer. Pterid. 18. 1901.
Pellaea atropurpurea f. *bifida* Hahne, in Fern Bull. 12:117. 1904, nom. nud.
Pellaea atropurpurea f. *furcata* Hahne, in Fern Bull. 12:117. 1904, nom. nud.
Cassebeera atropurpurea (L.) Farw. in Amer. Midl. Nat. 12:281. 1931.

Rhizome moderately stout, compact, decumbent, multicipital. Scales of the rhizome appressed and matted, rust colored in mass with the young tips light tan, these and those at the base of the stipes concolorous, tawny to rust colored, dull, linear-subulate, usually straight, the margins more or less dentate, the cells of the scale base small, mostly with oblique end walls, the apex attenuate, filiform, somewhat tortuous, appressed and entangled. Fronds 6–50 cm. long, erect, straight, stiff, dimorphic, the buds lanate. Stipe and rachis terete or elliptical, strongly pubescent to hispidulous, atropurpureous to black becoming gray with age, the stipe breaking irregularly, without perpendicular lines of articulation, the rachis of the mature frond atropurpureous to the terminal pinna. Blade 5.0 cm. long and 1.5 cm. broad to 25 cm. long and 18 cm. broad, elongate-triangular, once to tripinnate, clear to dark green, the lower pinnae usually 2 or more times as long as the upper, departing at broad angles to the rachis, the upper pinnae usually entire, subsessile or short stalked, the lower pinnae entire, deeply 1–3 lobed, or usually once pinnate with 3–15 segments, stalked, the pinna-stalks abruptly departing, not decurrent, the axils tan, the pinna-rachises up to 12 cm. long. Segments 1.0 cm. long and 0.5 cm. broad to 7.5 cm. long and 1.0 cm. broad, lanceolate or linear-oblong, entire or auriculate or ternately lobed, subcoriaceous, the undersurface often pubescent along the veins, the border broad, white or often opaque, crenulate, the fertile segments revolute, the apex muticous or mucronate, the mucro 0.25–1.50 mm.

long, flat, with a whitish margin contiguous with that of the segment. Sporangia with long stalks exceeding the length of the capsule, the annulus amber colored. Spores 32 per sporangium, ellipsoidal, rarely dumbbell shaped, yellow, with a prominent, rugose-lacy exospore.

Fig. 3. *Pellaea atropurpurea*, plant × ½; pinna; rhizome scale; section of rachis with pinna-stalks.



3. Distribution of *Pellaea atropurpurea* — X, literature records, see text.

P. atropurpurea is widely distributed throughout the eastern United States and wherever it grows it is usually found in abundance. I have observed the species at several stations in New England, Indiana, Minnesota, Texas and Missouri and while much variation exists in frond size the form is essentially uniform. Specimens transplanted from Gray Summit, Missouri, growing in the greenhouse over a period of three years, are more luxuriant than field specimens. These plants produced copious spores which were easily sown, and although only antheridia were produced, sporelings developed. In the eastern United States *P. atropurpurea* often grows on the same rocks or ledges as *P. glabella* var. *glabella* and although the two are readily distinguished when closely observed their relationship has been in question. The cytological and morphological data indicate the possibility of hybrids produced between *P. atropurpurea* and *P. glabella* var. *occidentalis*. The former, apogamous with 87 chromosomes, crossed with the normal sexual *P. glabella* var. *occidentalis*, may have given rise to *P. glabella* var. *glabella* to the east and *P. glabella* var. *simplex* to the west. Both of these varieties of *P. glabella* have chromosome numbers of 116 and are apogamous. Some morphological comparisons of the four entities are made in the following chart. It might be expected that the hybrids would bear a stronger resemblance to *P. atropurpurea* from which they would receive a triple genome.

	P. atropurpurea	*P. glabella* var. *glabella*	*P. glabella* var. *simplex*	*P. glabella* var. *occidentalis*
Frond length	6–50 cm.	4–36 cm.	1–20 cm.	1–5 cm.
Lines of articulation on the stipe	None	Occasionally	Rarely	Abundant
Pubescence on stipe and rachis	Abundant bicolorous hairs, hispid	Sparse bicolorous hairs	Sparse bicolorous hairs	Glabrous or rarely with bicolorous hairs
Length of pinna-stalk and rachis	Up to 120 mm.	Up to 50 mm.	Up to 10 mm.	Usually sessile, rarely up to 2 mm.
Number of segments per pinna	3–15	3–7	3–5	1 — this may be 2–3 lobed

A remark by Butters[24] in his studies of the pellaeas in the western United States pertaining to *Pellaea glabella* var. *occidentalis* is appropriate here " . . . it stands at one extreme of a series and *P. atropurpurea* at the opposite extreme".

From a morphological survey of the species in section PELLAEA, *P. atropurpurea* appears to be more closely related to *P. ternifolia* and *P. notabilis* which occur in Mexico. *P. atropurpurea* very probably originated from such an austral source and has spread to the north and east across the United States and into Canada.

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[24] Amer. Fern Journ. 7:82. 1917.

Cytological studies on the group seem to support the morphological evidence on the relationships between *P. atropurpurea* and *P. ternifolia*. Dr Irene Manton[25] reports a chromosome count of n & 2n = 87 for *P. atropurpurea* which is interpreted as a triploid pending the existence of a monoploid relative with 29 chromosomes. Dr. Britton confirms this report of 87 for *P. atropurpurea* from material collected by myself at Gray Summit, Missouri. He also reports counts of both n = 29 and n = 58 for *P. ternifolia*.

On exposed or shaded ledges and crevices of limestone cliffs, masonry walls or rocky loam of forest floor, at 300–3200 m.

Guatemala, northward in Mexico along Sierra Oriental, northeast across the United States to Vermont with outlying stations in the Black Hills of South Dakota, Keweenaw Point on Lake Superior, southeastern British Columbia and on the north shore of Lake Athabaska, Saskatchewan. Some of the specimens from the last two localities are depauperate but can be identified on the basis of the branching of the pinna-rachises, the slender, attenuate scales, prominent ornamentation of the spores and the long basal pinnae.

Two literature records from Colorado, indicated on the map by X, are taken from W. A. Webber in University of Colorado Studies, Biology Series No. 3:68. 1955.

Representative specimens:

CANADA. BRITISH COLUMBIA: *Eastham 11068* (MO, WTU, Univ.B.C.). SASKATCHEWAN: *Raup 6558* (CU, GH).

UNITED STATES. VERMONT: *Faxon* in 1877 (GH, NEBC). MASSACHUSETTS: *Bissell* in 1906 (GH, YU). CONNECTICUT: *Barnhart 603* (NY). RHODE ISLAND: *Greenman 2503* (MO). NEW YORK: *Eames 9016* (MO, US). NEW JERSEY: *Griscom 4817* (MO). PENNSYLVANIA: *Heller 711* (MO, US). DISTRICT OF COLUMBIA: *Maxon 6393* (GH, MO, NY). MARYLAND: 1896, *Waters* (US). VIRGINIA: *Adams & Wherry 2265* (MO, US). WEST VIRGINIA: *Allard 3592* (GH, NY, US). NORTH CAROLINA: *Oosting 35318* (MO, US). SOUTH CAROLINA: *Davis* in 1912, (MO). GEORGIA: *Harper 353* (GH, MO, NY, US); *Thorne & Muenscher 7685* (CU, UC). FLORIDA: *Small & Knight* in 1934 (GH, NY, US). ALABAMA: *D. S. & H. B. Correll 8284* (GH, NY, US). OHIO: *Demaree 11472* (MO). MICHIGAN: *Fernald & Pease 3035* (GH, NY, US). INDIANA: *Tryon 4439* (GH, MO, NY, US). KENTUCKY: *Palmer 17842* (GH, MO); *Smith et al. 3443* (GH, NY, US). TENNESSEE: *Pollard & Maxon 417* (GH, US). ILLINOIS: *Tryon 4652* (MO). MINNESOTA: *Schuster A5009* (MIN). MISSOURI: *Bush 5353* (GH, MO, US); 1899, Eureka, *Pauls* (MO); *Steyermark 65394* (F). ARKANSAS: *Palmer 6904* (MO, US). SOUTH DAKOTA: *Degener & Peiler 16701* (NY, US); *Rydberg 1190* (GH, US). NEBRASKA: *Webber Herb.* in 1889 (MO). KANSAS: *Horr E459* (GH, KANU, US). OKLAHOMA: *Houghton 3528* (GH, MO, NY). TEXAS: *Moore & Steyermark 3550* (GH, MO, US); *Mueller 8266* (GH, MO, NY, US). COLORADO: *Rogers 4970* (US). NEW MEXICO: *Maguire et al. 11653* (GH, US). ARIZONA: *Phillips 2799* (MO).

MEXICO. CHIAPAS: *Ghiesbreght 216* (F, GH, YU). CHIHUAHUA: *Stewart 2475* (GH). COAHUILA: *Stanford et al. 391* (MO, US); *Wynd & Mueller 358* (GH, MO, NY). NUEVO LEÓN: *C. H. & M. T. Mueller 362* (GH, US). PUEBLA: *Arsène 3548* (GH, MO, US). OAXACA: *Conzatti 1912* (F), *4279* (US). SONORA: *Hartman 357* (GH, NY, US). TAMAULIPAS: *Stanford et al. 943* (MO, US). VERACRUZ: *Bourgeau 3068* (GH, NY).

GUATEMALA. HEUHEUTENANGO: *Standley 62598* (F, US), *82761* (F).

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[25] Manton, I. Prob. Cytol. and Evol. of the Pterid. Cambridge Univ. Press, 1950.

4. PELLAEA TERNIFOLIA (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841.

Rhizome moderately stout, elongate, decumbent, multicipital. Scales of the rhizome appressed, scarcely entangled, brownish or the tips tan, these and those at the base of the stipes usually bicolorous with a narrow sclerotic stripe, subulate, straight or falcate, the margins usually irregularly dentate or erose, the cells of the scale base small, irregular, those above many times longer than broad, the apex attenuate, filiform, appressed and scarcely entangled. Fronds 4–50 cm. long, erect, straight and stiff, monomorphic, the buds sparsely pubescent, rarely lanate. Stipe and rachis convex or plane on the upper surface or sulcate, rarely terete, glabrous or rarely pubescent, glaucous, castaneous becoming darker with age, to ebony black, the stipe breaking irregularly without articulation lines, the rachis of the mature frond black or castaneous to the terminal pinna. Blade 3.0 cm. long and 0.5 cm. broad to 32 cm. long and 6 cm. broad, linear, lanceolate or elongate-triangular, once or bipinnate, clear or grayish green, the pinnae of nearly the same length or the lower longer, departing at broad angles to the rachis, entire, ternate, or with 3–11 segments, subsessile or stalked, pinna-stalks not decurrent, the axils colored as the rachis or tannish, the pinna-rachises up to 2 cm. long. Segments 0.5 cm. long and 0.5 cm. broad to 4 cm. long and 1.0 cm. broad, lanceolate to narrowly oblong, entire or ternately divided, subcoriaceous, the borders whitish, crenulate, mucronate, the mucro 0.5–1.5 mm. long, flat or reflexed, with a whitish margin contiguous with that of the segment. Sporangia long stalked, the annulus amber colored; glands with ceraceous indument may occur among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent, rugose exospore.

P. ternifolia is a critical species for it bears relationships to several others and problems relevant to them. The series from this species through *P. brachyptera* shows greater cohesion than any other in the genus. The entities differ by quantitative characters and their ranges for the most part are geographically distinct. The pinnae of *P. ternifolia* var. *Wrightiana* are longer and more dissected than those of *P. ternifolia* var. *ternifolia* and are further expanded in the following two species.

Two chromosome numbers have been reported for *P. ternifolia* var. *ternifolia* by Dr. Britton. A collection from Cuernavaca, State of Morelos in Mexico, *R. M. & A. F. Tryon 5105*, and one from El Pedregal on the south edge of Mexico City, *R. M. & A. F. Tryon 5146*, have chromosome numbers of n = 29. A collection from Valle de Bravo, State of Mexico, was reported as n = 58 and another from Cuernavaca was a probable polyploid although the number was not definitely established. It is unfortunate that both of the polyploid numbered collections have been lost.

P. ternifolia is also suspected of entering into crosses which have produced *P. atropurpurea* and possibly *P. Pringlei*. The range of *P. ternifolia*, though more extensive, resembles that of *P. ovata* but there is no evidence from spore counts, as exists in the latter, of a wide-ranging apogamous strain.

Key to Varieties

Blade linear, pinnate or pinnate-pinnatifid; pinnae ternate or entire, without pinna-rachises; southern Texas and Arizona southward along the Cordillera to central Chile, Dominican Republic, Hawaiian Islands. .... 4A. var. *ternifolia*, p. 150

Blade linear to usually narrowly triangular, bipinnate; pinnae lobed or divided into 3–11 segments, pinna-rachises 4–20 mm. long; southern Oklahoma to northern Mexico............ 4B. var. *Wrightiana*, p. 153

4A. Pellaea ternifolia var. ternifolia. Fig. 4A. Map 4A.

Pteris ternifolia Cav. Descr. Pl. 266. 1802. (Lectotype by C. Christensen in Dansk Bot. Ark. 9:22. 1937: *Née,* Peru MA; Isotype: F!).
Pteris peruviana Poir. in Lam. Ency. Meth. Bot. 5:718. 1804. (Holotype: *Joseph Jussieu,* Peru P!, Photo: GH!).
Pteris subverticillata Sw. Syn. Fil. 103. 1806, based on *Pteris ternifolia* Cav.
Pteris triphylla Bertero, in Merc. Chil. 16:748. 1829, nom. nud.; ex Colla, Herb. Pedem. 6:199. 1836. (Holotype: *Bertero,* in 1828, TO; Isotypes: GH! SGO). Reference as to the type from Looser, in Rev. Univ. (Univ. Cat. Chile) 25:111. 1940; as to the Colla reference, Pichi-Sermolli, in Webbia 8:135. 1951.
Allosorus subverticillatus (Sw.) Presl, Tent. Pterid. 153. 1836.
Platyloma ternifolia (Cav.) J. Sm. in Bot. Mag. 72: Comp. 21. 1846.
Allosorus ternifolius (Cav.) Kze. ex Kl. in Linnaea 20:339. 1847.
Pellaea Weddelliana Fée, in Mém. Soc. Mus. Hist. Nat. Strasb. 5:74. 1857. (Mém. Fam. Foug. 8). (Lectotype: *Weddell 3778* K!, Isotypes: P! YU!).
Pellaea lanuginosa Fée, in Mém. Soc. Hist. Nat. Strasb. 5:114. 1857. (Mém. Fam. Foug. 8) nom. provis. (Holotype: *Schaffner 321* P).
Pellaea mucronata Fée, Cat. Meth. Foug. Lycop. Mex. 8. 1857. (Mém. Fam. Foug. 9) nom. nud., not (D. C. Eaton) D. C. Eaton, in Torr. U. S. & Mex. Bound. Bot. 233. 1859. (Isotype: *Schaffner 150* YU!).
Cheilanthes lanuginosa (Fée) Moore, Ind. Fil. 255. 1861; not Mett. ex Hook. Syn. Fil. 2:99. 1858, nor Mart. & Gal. in Mém. Acad. Brux. 15:75. 1842.
Cheilanthes Weddelliana (Fée) Moore, Ind. Fil. 255. 1861.
Cheilanthes ternifolia (Cav.) Moore, loc. cit.
Nothochlaena ternifolia (Cav.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.
Adianthum ternatum Sessé & Moc. Pl. Nov. Hisp. 182. 1887–90; ed. 2. 169. 1893, not Humb. & Bonpl. ex Willd. 1810.
Pellaea ternifolia var. *petiolulata* C. Chr. in Ark. Bot. 20: 18. 1926. (Holotype: *Asplund 3071* UPS, Isotype: US!).
Cassebeera ternifolia (Cav.) Farw. in Amer. Midl. Nat. 12:281. 1931.
Pellaea Brandegeei C. C. Hall, in Amer. Fern Journ. 37:111. 1947. (Holotype: *Brandegee,* Mexico UC!, Isotype: US!).

Scales of the rhizome and base of the stipes bicolorous with a slender central sclerotic stripe usually narrower than the border, the margins entire at the base, dentate above. Stipe and rachis plane on the upper surface or sulcate, atropurpureous or black. Blade linear to narrowly lanceolate, once pinnate. Pinnae ternate or entire, sessile or subsessile, without pinna-rachises. Without glands among the sporangia.

Several segregates of *P. ternifolia* var. *ternifolia* have been made on differences in the form of the pinnae, length of the pinna-rachises and serration and color of the scales. Such variations are not sufficiently clear for taxonomic recognition although they are of interest in the dynamics of the species. The segregates, *P.*

Fig. 4A. *Pellaea ternifolia* var. *ternifolia,* plant × ½; pinna; rhizome scale.

Brandegeei at the southern end of Baja California and *P. Weddelliana* in Bolivia and northern Argentina show slight differences which would be expected in populations isolated from the main geographic range of the species. Collections from several localities in central Mexico which have entire pinnae, pubescent rachises and lax fronds are presumably Fée's *P. lanuginosa.* This may be cytologically distinct for a pubescent specimen from Valle de Bravo is reported to have a chromosome number of n = 58. Two other collections of *P. ternifolia* var. *ternifolia* from the vicinity of Mexico City are reported as n = 29.

In crevices or among igneous rocks, on dry earthen walls in Peru, in sun or semi-shade, at 200–4000 m.

4A. Distribution of *Pellaea ternifolia* var. *ternifolia*, 4B. var. *Wrightiana*.

Southern Arizona and Texas; Mexico; Guatemala; Nicaragua; Hispaniola; Venezuela, Colombia to Argentina; Hawaiian Islands.

Representative specimens:

UNITED STATES. ARIZONA: *Phillips et al. 2565* (US). TEXAS: *E. J. Palmer 34165* (GH, MO, NY); *R. M. & A. F. Tryon 5097* (GH, K, MO, MEXU, U, UC, US, UT).

MEXICO. BAJA CALIFORNIA: *Jones 27013* (MO, NY, UC, US); Cape Region, in 1893, *Brandegee* (UC). CHIHUAHUA: *Pringle 920* (F, GH, MO, US); *E. Palmer 452* (GH, MO, NY, US, YU). COAHUILA: *Wynd & Mueller 574* (GH, MO, NY, US). DURANGO: *Pennell 18258* (F). GUANAJUATO: Sept. 1900, *Dugès* (GH). GUERRERO: *Hinton 10490* (F, MO, NY, US). HILDALGO: *Clokey 1892* (MO). JALISCO: *McVaugh 12998* (US); *E. Palmer 764* (US, YU). MEXICO: *Lyonnet 26* (GH, MO, NY, US); *Matuda 26923* (US); *R. M. & A. F. Tryon 5137, 5141* (MEXU, MO), *5146* (MEXU, MO, US). MICHOACÁN: *Arsène 1975* (US). MORELOS: *Orcutt 3827* (GH, MO, US); *R. M. & A. F. Tryon 5102* (MEXU, MO). OAXACA: *Conzatti 1401* (GH). PUEBLA: *Arsène 1995* (GH, MO, US). QUERÉTARO: *Arsène 10654* (US). SAN LUIS POTOSÍ: *Parry & Palmer 982* (F, MO, NY, US, YU). SINALOA: *Gentry 6434* (MO). SONORA: *White 4221* (GH). TLAXCALA: *Hernández-Xolocotzl 334* (US); *Sharp & Hernández 44445* (US). VERACRUZ: *Seaton 279* (F, GH, US). ZACATECAS: *Rose 2792* (US).

GUATEMALA: *Skutch 806* (GH, UC); *Standley 58350* (F, US).

NICARAGUA: *Standley 11005* (F).

DOMINICAN REPUBLIC: *Ekman 11706* (NY, US); *R. H. & E. S. Howard 9137* (GH, MO, NY, US).

VENEZUELA. MÉRIDA: *Gehriger 251* (US).

COLOMBIA. BOYACÁ: *Fosberg 22210* (US). CUNDINAMARCA: *Pennell 2548* (F, GH, MO, NY, US). VALLE: *Cuatrecasas 20829* (F, US). CAUCA: *Killip 6882* (GH, NY, US). MAGDALENA: *Seifriz 471* (US). NORTE DE SANTANDER: *Garganta 1225* (F). SANTANDER: *Killip & Smith 18751* (F, GH, NY, US).

ECUADOR. AZUAY: *Rose et al. 22872* (NY, US). IMBABURA: *Mexia 7403* (UC, US). LOJA: *Fosberg & Giler 23112* (US). PICHINCHA: *Heilborn 177* (GH, US). TUNGURAHUA: *Pachano 114* (US).

PERU. Near Guamantanga, Guarimaya Valley, *Née* (F). AREQUIPA: *Pennell 13075* (F, GH, NY, US). CUZCO: *Herrera 3172* (F). JUNÍN: *Killip & Smith 21817* (NY, US). LA LIBERTAD: *Stork & Horton 9997* (F, UC). LIMA: *Macbride & Featherstone 286* (F, US). PUNO: *R. S. Williams 2633* (GH, NY, US).

BOLIVIA. CHUQUISACA: Tomina, 1845–46, *Weddell 3778* (K, P, YU). ORURA: *Buchtien 1139* (US). POTOSÍ: *Asplund 3071* (UPS, US), *4841* (US). LA PAZ: *Bang 91* (GH, MO, NY, UC, US); *Rusby 323* (GH, US). TARIJA: *Fiebrig 3138* (GH, P, UC, US).

ARGENTINA. BUENOS AIRES: *Eyerdam et al. 23403* (GH, UC). CATAMARCA: *Jörgensen 1251* (GH, MO, UC, US). CORDÓBA: *Hieronymus 475* (NY, US). JUJUY: *Schulz 972* (GH); *West 6249* (US). LA RIOJA: *Hunziker 5278* (MO). SALTA: *Venturi 9983* (GH). TUCUMÁN: *Venturi 10428* (GH, MO.)

CHILE. ANTOFAGASTA: *Johnston 5305* (GH, US). CAUTÍN: *Claude-Joseph 2658* (US). O'HIGGINS: May 1828, *Bertero* (GH). VALDIVIA: *Hollermayer 1898* (MO, US).

HAWAIIAN ISLANDS. HAWAII: *Mann & Brigham 262* (GH, MO, US). MAUI: *Degener & Wiebke 3975* (GH, MO, US). OAHU: *Degener 10419* (MO, US).

4B. PELLAEA TERNIFOLIA var. **Wrightiana** (Hook.) A. F. Tryon, comb nov. Fig. 4B. Map 4B.

Pellaea Wrightiana Hook. Sp. Fil. 2:142. 1858. (Holotype: *Wright 2130* K!, Isotypes: GH! NY! US! YU!).

Cheilanthes mucronata var. *Wrightiana* (Hook.) Moore, Ind. Fil. 248. 1861.

Scales of the rhizome and base of the stipes bicolorous, the central sclerotic stripe as broad or broader than the border, the margins dentate to the base. Stipe

Fig. 4B. *Pellaea ternifolia* var. *Wrightiana*, plant × ½; pinna; rhizome scale.

and rachis sulcate, castaneous, becoming darker with age. Blade narrowly triangular, bipinnate. Pinnae lobed or divided into 3–11 segments, usually stalked, the pinna-rachises 0.4–2.0 cm. long. Glands with ceraceous indument rarely occur among the sporangia.

P. ternifolia var. *Wrightiana* has formerly been treated as a distinct species. It is essentially similar to *P. ternifolia* var. *ternifolia* in the architecture of the blade and is considered a northern extension of the species having quantitative differences not sufficient for specific separation.

In crevices of igneous or limestone rocks or on rocky or gravelly hillsides, full sun or partial shade, at 1400–2300 m.

Oklahoma to Arizona; northern Mexico.

Representative specimens:

UNITED STATES. OKLAHOMA: *Waterfall 6456* (GH). TEXAS: *Moore & Steyermark 3019* (GH, MO, NY, US); *Mueller 8265* (GH, MO, US); *E. J. Palmer 34260* (F, MO, NY); *Reverchon 1216* (F, GH, MO, NY, US); *R. M. & A. F. Tryon 5041* (MO, US) *5096* (GH, K, MO, U, US). NEW MEXICO: *Eastwood 8266* (GH, US); *Goodding 766* (GH, NY, US); Dec. 1880, *Rusby* (MO, US, YU); 1851, *Wright 2130* (GH, K, NY, US, YU). ARIZONA: *Blumer 1867* (F, NY, US); Sept. 1880, *Engelmann* (MO); *B. & R. R. Maguire 12027* (US); *Phillips & Reynolds 2943* (GH, US).

MEXICO. BAJA CALIFORNIA: April 1889, *Brandegee* (GH, US); *Gentry 4283* (GH, MO). CHIHUAHUA: *Johnston 8090* (GH); *Pennell 19209* (US). COAHUILA: *Johnston & Muller 1309* (GH). SONORA: 1895, *Druery* (US).

5. PELLAEA LONGIMUCRONATA Hook. Sp. Fil. 2:143. 1858. (Holotype: *Wright 2131 K!*, Photo: GH!, Isotypes: GH! US! YU!). Fig. 5. Map 5

Pellaea Wrightiana var. *longimucronata* (Hook.) Davenp. Cat. Davenp. Herb. Suppl. 46. 1883.
Pellaea truncata Goodding, in Muhlenb. 8:94. 1912. (Holotype: *Goodding 977* US!).
Cassebeera ternifolia var. *longimucronata* (Hook.) Farw. in Amer. Midl. Nat. 12:282. 1931.

Rhizome moderately stout, elongate, decumbent, multicipital. Scales of the rhizome and base of the stipes appressed, brown, bicolorous, with a central sclerotic stripe usually broader than the border, subulate, straight or falcate, the margin erose-dentate, the cells of the border trapezoidal, usually not more than five times longer than broad, the apex dentate, not attenuate. Fronds 12–38 cm. long, erect, straight and stiff, monomorphic, the lower pinnae often sterile, the upper fertile, the buds sparsely pubescent. Stipe and rachis sulcate, glabrous or nearly so, usually glaucous, castaneous becoming darker with age, the stipe breaking irregularly without articulation lines, the rachis of the mature frond castaneous to the terminal pinna. Blade 8 cm. long and 4 cm. broad to 22 cm. long and 12 cm. broad, triangular, acuminate, bipinnate, rarely tripinnate, grayish green, the lower pinnae longer, departing at broad angles to the rachis, once pinnate with 9–21 segments, rarely bipinnate, sessile or short stalked, the pinna-stalks not decurrent, the axils colored as the rachis, the pinna-rachises up to 7 cm. long. Segments 0.3 cm. long and 0.1 cm. broad to 1.5 cm. long and 1.0 cm. broad, narrowly oblong to oval, entire, subcoriaceous, the border narrow, white, crenulate or dentate, mucronate, the mucro 0.5–2.0 mm. long, flat or reflexed, green at the base, with a white margin extending into the attenuate apex and contiguous with the borders of the segment. Sporangia usually long stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, the exospore of short, scarcely prominent rugae.

During field studies made in July and August of 1950 in southern Texas, New Mexico and Arizona six species of the section were collected and *P. longimucronata* was most frequently encountered. It grows in extremely xeric habitats often devoid of other vegetation.

In clefts of igneous rocks or among boulders or gravelly soil, in open sun, at 1250–2000 m.

Texas to Colorado, Arizona, Utah, Nevada; northern Mexico.

Fig. 5. *Pellaea longimucronata*, plant × ½; pinna; rhizome scale.

Representative specimens:

United States. texas: *Correll 13799* (MO), *15049* (MO); *Hinckley 2585* (GH, NY, US); *R. M. & A. F. Tryon 5086* (GH, MO, US); *Waterfall 4568* (GH, MO). colorado: April 24, 1874, *Brandegee* (F, MO); Sept. 25, 1874, *Engelmann* (MO). new mexico: Sept. 10, 1880, *Rusby* (F, GH, MO, NY, US, YU); *R. M. & A. F. Tryon 5087* (GH, K, MEXU, MO, U, US); 1897, *Wooton 99* (MO, NY, US); 1851–52, *Wright 2131* (GH, K, NY, US). utah: *Gould 1740* (NY, US); *Palmer 497* (NY). arizona: *Blumer 1970* (GH, US); Mule Mts., Aug. 1911, *Goodding 977* (US); *Palmer 649* (F, MO, YU); March 11, 1884, *Pringle* (F, US); *Rothrock 464* (F, GH, MO); *R. M. & A. F. Tryon 5099* (MO). nevada: *Clokey 8257* (F, MO, NY); *Goodding 737* (F, GH, MO, NY, US); *Jones 5055* (MO, NY).

Mexico. baja california: April 20, 1889, *Brandegee* (GH, NY); *Palmer 554* (GH). sonora: *E. A. Phillips 511* (GH).

6. Pellaea mucronata (D.C. Eaton) D. C. Eaton, in Torr. U. S. & Mex. Bound. Bot. 233. 1859, not Fée, Cat. Meth. Foug. Lycop. Mex. 8. 1857 (Mém. Fam. Foug. 9) nom. nud.

Rhizome moderately stout, compact or somewhat elongate, decumbent, multicipital. Scales of the rhizome and base of the stipes appressed, brown, bicolorous with a central sclerotic stripe as broad or broader than the border, straight or falcate, subulate, sparsely dentate to entire at the base, dentate to erose above, the cells of the border with oblique end walls, usually not more than five times longer than broad, the apex filiform, tortuous, entangled. Fronds 6.5–43.0 cm. long, erect, stiff, monomorphic, the lower pinnae sometimes sterile, the upper fertile, the buds strongly pubescent or lanate. Stipe and rachis sulcate or plane on the upper surface, glabrous or nearly so, glaucous, castaneous, the stipe often bent or curled, breaking irregularly without articulation lines, the rachis of the mature frond castaneous to the terminal pinna. Blade 3.5 cm. long and 1.0 cm. broad to 25 cm. long and 18 cm. broad, ovate-triangular to rhomboid, acuminate, often abruptly so, bi-to tripinnate, rarely quadripinnate, grayish green, the central or lower pinnae longest, departing at broad or acute angles to the rachis, once pinnate or bipinnate with few to 40 segments, subsessile or short stalked, the pinna-stalks not decurrent, the axils colored as the rachis, the pinna-rachises up to 10 cm. long, exceeding the length of the segments several times. Segments 0.2 cm. long and 0.1 cm. broad to 1.2 cm. long and 0.6 cm. broad, narrowly oblong, entire or ternate, subcoriaceous, the border undifferentiated, crenate, mucronate, the mucro 0.25–1.50 mm. long, flat, thickened, green at the base, the apex lutescent, distinct from the revolute borders of the segment. Sporangia short stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium, mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent rugose exospore.

Key to Varieties

Pinnae distant, not imbricate, at broad angles to the rachis; pinnules few to 40 per pinna, usually ternate; northern California to Baja California and coastal islands, usually below 1800 m. .... 6A. var. *mucronata*, p. 158

Pinnae imbricate, especially on the apical portion of the frond, ascending at acute angles to the rachis; pinnules fewer than 20 per pinna, usually entire; Sierra Nevada and southern California, usually above 1800 m. .... 6B. var. *californica*, p. 161

This Californian species exhibits a plasticity of form as great as that of the wider ranging *P. ternifolia*. It occurs among igneous rocks in arid or semi-arid montane regions of the state and is undoubtedly influenced by the topographic and climatic diversities. Mason's[26] observations, especially pertaining to this region,

[26] Madroño 8:209, 241. 1946.

on the effect of topography and climate on the distribution of restricted species helps to interpret the variations of this fern. In southern California Ewan[27] has studied *P. mucronata*, particularly those plants occurring at the higher altitudes. He considers *P. mucronata* var. *californica* to be derived from *P. mucronata* var. *mucronata* through isolation and consequent morphological changes in extreme environments. Less distinct variations in collections of var. *mucronata* from Kern, Tulare and Fresno counties have small, closely set pinnules and have been noted by Maxon.[28] Other specimens from northern California are distinctive in having compound pinnules with 3–11 segments. A few specimens, two of which are cited in the treatment of the next species, have entire pinnules and lax pinnae intermediate between *P. mucronata* var. *mucronata* and *P. brachyptera* and are possibly hybrids.

6A. Pellaea mucronata var. mucronata Fig. 6A. Map 6A.

Allosorus mucronatus D. C. Eaton, in Amer. Journ. Sci. 22:138. 1856. (Holotype: *Major A. B. Eaton*, near Bay of San Francisco, Calif. YU!, Photo: GH!).

Pelleae longimucronata var. *minor* Hook. Sp. Fil. 2:143. 1858, nom. nud. based on *Major A. B. Eaton*, Bernica, Calif. K, Isotype: GH!.

Pellaea ornithopus Hook. Sp. Fil. 2:143. 1858. (Holotype: *Hartweg 2042* K!, Photo: GH!, Isotypes: GH! P!).

Cheilanthes mucronata (D.C. Eaton) Moore, Ind. Fil. 45, 248. 1861.

Allosorus ornithopus (Hook.) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Cassebeera ternifolia var. *ornithopus* (Hook.) Farw. in Amer. Midl. Nat. 12:282. 1931.

Cassebeera ternifolia var. *mucronata* (D.C. Eaton) Farw. loc. cit. 1931.

Cassebeera ternifolia var. *stipitata* Farw. loc. cit. (Holotype: *Blaisdell*, in 1881, MICH!).

Fronds 6.5–43.0 cm. long. Blade 3.5 cm. long and 1.0 cm. broad to 25 cm. long and 18 cm. broad, ovate to rhomboid, bi- or tripinnate, rarely quadripinnate, more or less plane, the apex abrupt or acuminate. Pinnae linear to ovate, not imbricate, at wide angles to and widely spaced on the rachis, those of the mid-region often longer than the basal, with few to 40 segments per pinna. Segments widely spaced on the pinna-rachises, usually ternate.

A collection of Ezra C. Knopf from Santa Catalina Island bears the accompanying information —

> "An infusion of the dried leaves of this plant is much prized by the Spanish, Mexicans and some of the white residents, as a tea. I have drunk it and found it quite palatable. It is said to be good for the kidneys and as a blood purifier. After the rainy season is past the plant dries and can be picked any time during the summer. The Indian name is Calagula."

In crevices of igneous rocks or among boulders, full sun or semishade, at 20–2000 m.

California; Baja California.

Representative specimens:

United States. california: *Alexander & Kellogg 1993* (MO); *Austin 221* (MO, US); *Baker 2613* (GH, MO, US); San Diego, 1881, *Blaisdell* (MICH); *H. E. Brown 268* (F, MO, US); *Clokey 4840* (MO, P); Bay of San Francisco, *Major A. B. Eaton* (YU); Oct. 1880, *Engelmann* (MO); *Fosberg R84* (F, MO, US); *Hansen 657* (MO, NY, P); *Hartweg 2042* (GH, K, P); *Heller 7816* (GH, MO, NY, P, US); *Kellogg & Harford*

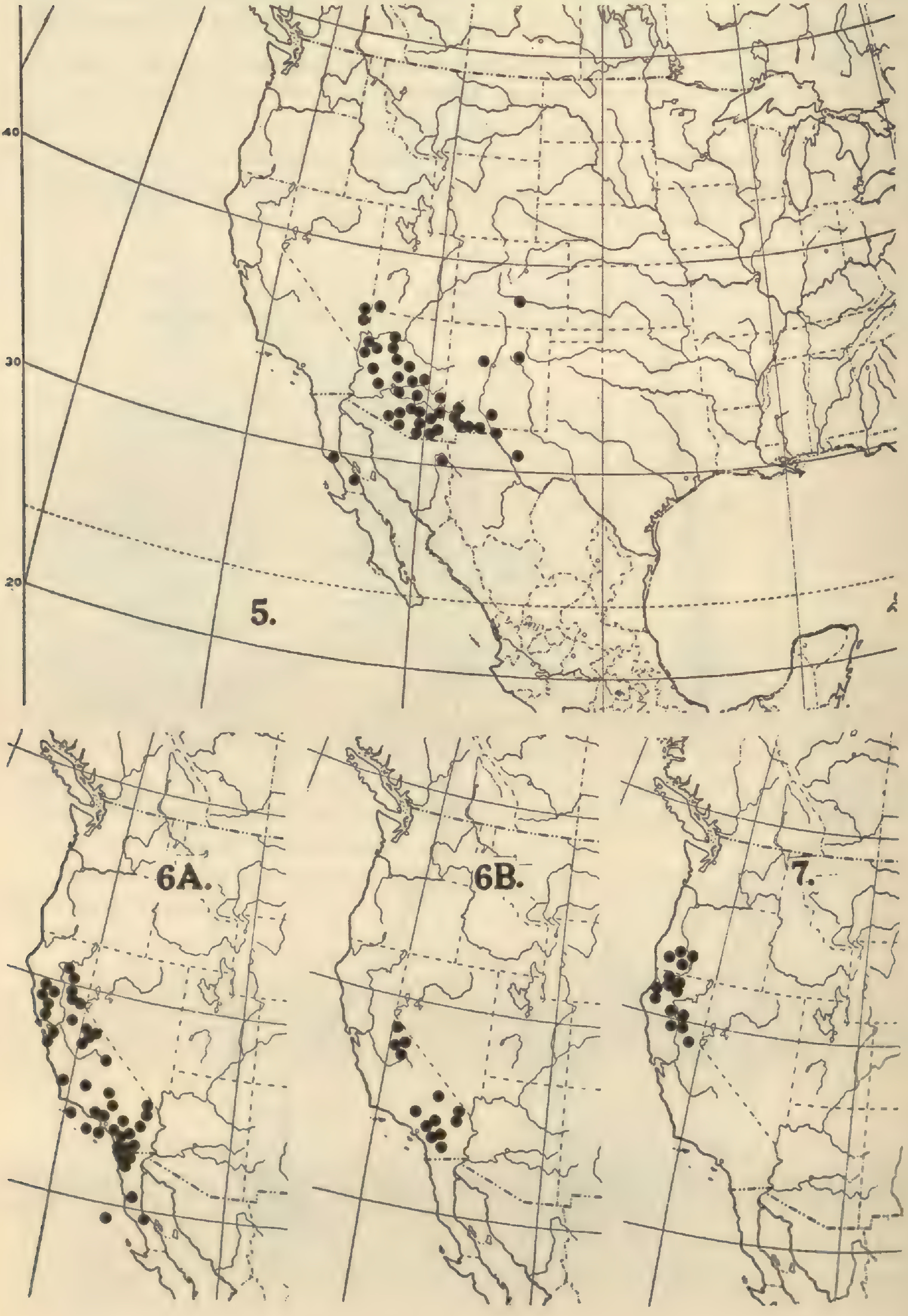
[27] Journ. Wash. Acad. Sci. 25:363–370. 1935.

[28] Proc. Biol. Soc. Wash. 30:179. 1917.

1170 (MO, US, YU); *McKelvey 5053* (GH, US); *Palmer 424* (GH, MO); July 14, 1882, *Pringle* (GH, MO, US); *Torrey 595* (GH, NY, US); *R. M. & A. F. Tryon 5058* (GH, K, MEXU, MO, U, UC, US, UT).

MEXICO. BAJA CALIFORNIA: *Wiggins 9821* (US); *Wiggins & Gillespie 4151* (GH, MEXU, MO, US). GUADALUPE ISLAND: *Palmer 100* (GH, MO, NY YU).

Fig. 6A. *Pellaea mucronata* var. *mucronata*, plant × ½; pinna; rhizome scale.



5. Distribution of *Pellaea longimucronata*, 6A. Distribution of *Pellaea mucronata* var. *mucronata*, 6B. var. *californica*, 7. Distribution of *Pellaea brachyptera*.

6B. Pellaea mucronata var. californica (Lemmon) Munz & Johnston, in Amer. Fern Journ. 12:106. 1922. Fig. 6B. Map 6B.

Pellaea Wrightiana var. *californica* Lemmon, Ferns Pacific Coast, 10. 1882. (Lectotype: *Lemmon*, May 30, 1876, UC!, Isotypes: F! GH! US!).
Platyloma bella Moore, in Gard. Chron. 213. 1873. (Holotype: Hort. Veitch. Chelsea, from California K!, Photo: GH!).
Pellaea bella (Moore) Baker, Syn. Fil. 477. 1874.
Pellaea Wrightiana var. *compacta* Davenp. Cat. Davenp. Herb. Suppl. 46. 1883. (Holotype: *W. G. Wright* in 1879, GH!).
Allosorus bellus (Moore) O. Ktze. Rev. Gen. Pl. 2:806. 1891.
Pellaea compacta (Davenp.) Maxon, in Proc. Biol. Soc. Wash. 30:183. 1917.

Fig. 6B. *Pellaea mucronata* var. *californica*, plant × ½; pinna; rhizome scale.

Fronds 9–33 cm. long. Blade 5.5 cm. long and 2.0 cm. broad to 18 cm. long and 8 cm. broad, narrowly deltoid, bipinnate, often conduplicate, acuminate. Pinnae linear, imbricate, usually closely appressed and at acute angles to the rachis, those of the mid-region as long as the basal, with few to 20 segments per pinna. Segments closely placed on pinna-rachises, usually entire.

Some of the earliest collections of this variety from the San Bernardino mountains were made by W. G. Wright. Specimens which he sent to Eaton and Gray are accompanied by letters remarking on the characteristics of the plants which distinguish them from *P. mucronata* var. *mucronata*. His allusion to the pinnae standing back together much as the wings of a bird is a striking one and the character is often apparent in herbarium specimens. The stipe may be curled or bent at the base and proportionately longer than the blade for the plants often grow from the base of boulders or among rocks.

In the absence of a specimen with sufficient data to unquestionably indicate the type I am choosing the above-cited Lemmon specimen. This sheet from the Lemmon Herbarium, collected prior to 1882, is not labeled var. *californica* but bears two tickets—one with locality data and the other labeled "*Pellaea Wrightiana* var. *compacta* Dav." in Lemmon's handwriting. He apparently added the name after 1883. A collection of 1888 from the same locality, which has been named by Lemmon var. *californica*, matches the earlier one and would indicate his concept of the variety.

On talus, among loose rocks or in rocky woods, open sun or shade, at 1800–3000 m.

California.

Representative specimens:

United States. california: *Abrams 2684* (GH, MO, NY, US); *Alexander & Kellogg 2948* (UC); *Dudley & Lamb 4648* (F, UC); *Ewan 9828* (US); *Hoover 1563* (UC, US); Mt. San Bernardino, May 30, 1876, *J. G. Lemmon* (F, GH, UC, US) *B. S. & W. F. Parish 511* (F, GH, US); *R. M. & A. F. Tryon 5061* (GH, K, MEXU, MO, U, UC, US, UT); San Bernardino Mts., 1879, *W. G. Wright* (GH).

7. Pellaea brachyptera (Moore) Baker, Syn. Fil. 477. 1874

Fig. 7. Map 7

Platyloma brachyptera Moore, in Gard. Chron. 141. 1873. (Holotype: Hort. Veitch. Chelsea, from Calif. K!, Photo: GH! US!).

Pellaea ornithopus var. *brachyptera* (Hook.) D.C. Eaton, in Bull. Torr. Bot. Club 4:11. 1873.

Allosorus brachypterus (Moore) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome moderately stout, elongate, decumbent, multicipital. Scales of the rhizome and base of the stipes appressed, ruddy brown, bicolorous, the central sclerotic stripe narrower than the border, often not extending into the scale apex, linear, straight or tortuous, strongly dentate, the cells of the border with oblique end walls, 5–10 times longer than broad, the apex filiform, tortuous, entangled. Fronds 9–39 cm. long, stiff, bent or straight, monomorphic, the buds pubescent. Stipe and rachis sulcate, glabrous or nearly so, glaucous, castaneous, the stipe wiry, often curled, breaking irregularly without articulation lines, the rachis of the

mature frond castaneous to the terminal pinna. Blade 5 cm. long and 1 cm. broad to 20 cm. long and 4 cm. broad, linear, bipinnate, rarely tripinnate, grayish green, the pinnae of nearly the same length, ascending at acute angles and appressed to the rachis, pinnate with 5–13 segments, subsessile or short stalked, the pinna-stalks not decurrent, the axils colored as the rachis, the pinna-rachises up to 2 cm. long, usually shorter than the segments. Segments 0.5 cm. long and 0.2 cm. broad to 2.0 cm. long and 0.4 cm. broad, linear, subcoriaceous, the border strongly revolute, undifferentiated, crenate, mucronate, the mucro 0.25–1.0 mm. long, flat, thickened, green at the base, the apex lutescent, distinct from the revolute borders of the segment. Sporangia short stalked, the annulus amber colored, glands with ceraceous indument occurring among the sporangia. Spores 64 per sporangium,

Fig. 7. *Pellaea brachyptera*, plant × ½; pinna; rhizome scale.

mostly tetrahedral-globose, yellow-tan, with a sparse, scarcely prominent, rugose exospore.

In the search for unusual ferns for English stoves this species was brought from California by Veitch & Sons of Chelsea. The type material grown in the greenhouse in England is more robust than any of the collections from the field. Specimens at the Gray Herbarium and at Yale include some field notes of H. N. Bolander in which he observes that plants from rocks moistened by spray have larger, more numerous segments than those growing among dry rocks. From these observations on the effect of the environment D. C. Eaton concluded that *P. brachyptera* be given only varietal status.

Bolander's collection from the Sierras at 4,000 feet, in 1869 (MO, YU) and that of *Kellogg & Harford 1169* (GH, US) are difficult to place as they are intermediate between *P. brachyptera* and *P. mucronata* var. *mucronata*. These two are obviously closely related for their differences are mainly quantitative. The former has shorter pinnae, longer segments, more tortuous rhizome scales as well as a range farther north in California than *P. mucronata* var. *mucronata*. Morphologically the two entities are better defined than in the case of *P. ternifolia* var. *ternifolia* and var. *Wrightiana*.

On talus slopes or basalt or serpentine rock outcrops, at 800–2000 m.

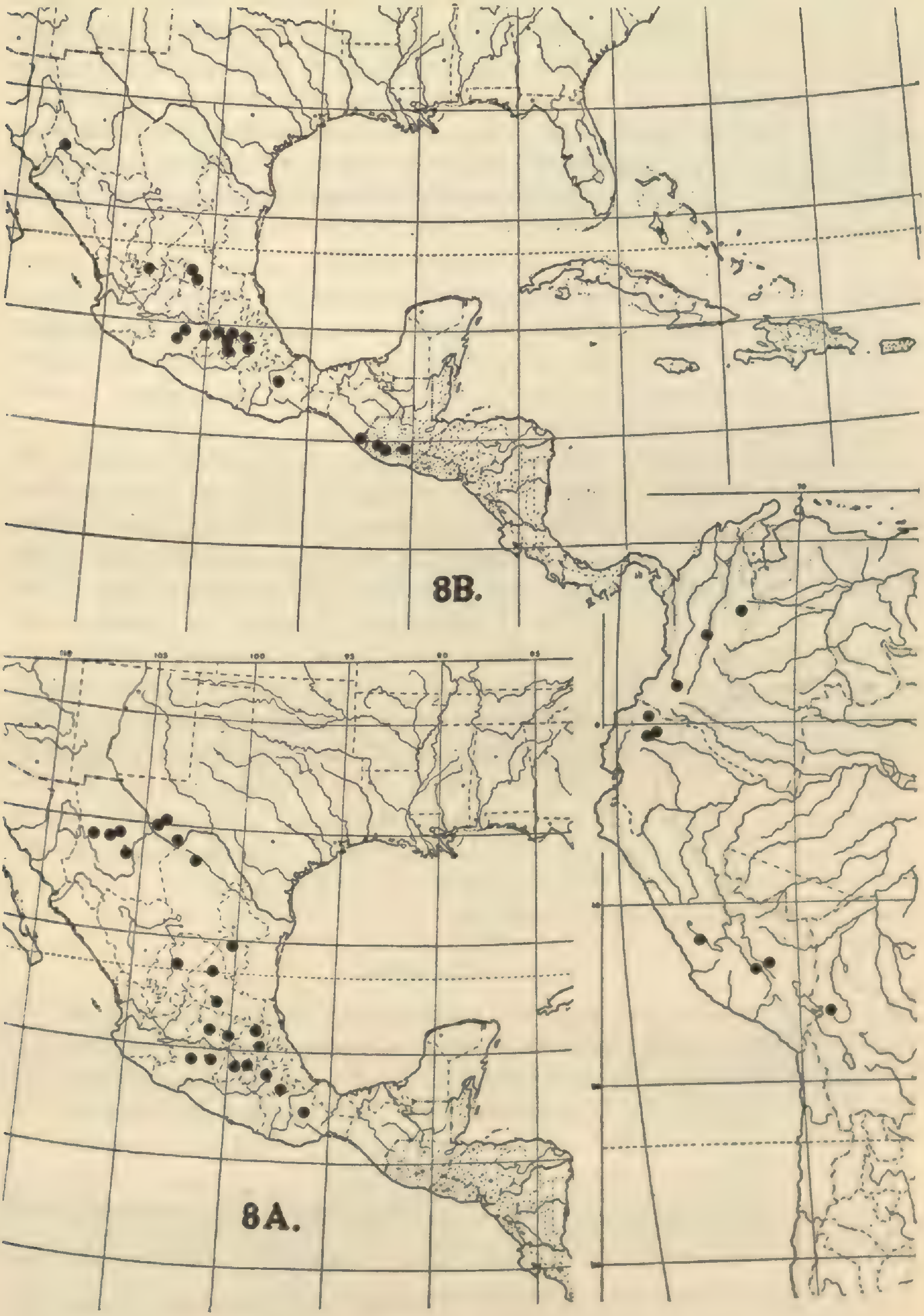
California, Oregon.

Representative specimens:

United States. california: *Constance & Rollins 2933* (GH, MO, US); *Copeland 401* (F, GH, MO, NY, P, US); Aug. 1880, *Engelmann* (MO); July 15, 1907, *Heller & Kennedy* (F, MO, NY, US); *Ownbey & Brown 2424* (GH, MO, NY); *Ownbey & Meyer 2198* (MO, NY, US); *Wheeler 2744* (GH, MO, NY, US). oregon: *Applegate 2608* (US); July 5, 1887, *Howell* (F, GH, MO, OSC, US, YU); *Thompson 13066* (GH, MO, NY, US).

8. Pellaea sagittata (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841.

Rhizome moderately stout, compact, decumbent, multicipital. Scales of the rhizome appressed and matted, tan to rust colored, concolorous, dull, elongate lanceolate-triangular, usually cordate, straight or nearly so, the margins irregularly dentate, the cells short rectangular or with oblique end-walls or elongate, the apex filiform, more or less tortuous, scales of the base of the stipes and buds appressed, tawny, concolorous, dull, broadly ovate-lanceolate, cordate or pseudopeltate, straight, the margin erose, the cells irregular, sinuous or curved, the apex filiform, tortuous. Fronds 16–78 cm. long, erect, straight, stiff, approximate, dimorphic, the sterile frond shorter and usually with larger segments than the fertile, the buds paleaceous. Stipe and rachis convex or plane on the upper surface, glabrous or puberulous, straw colored to ruddy tan, or mottled, becoming darker with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous, often green in the juvenile frond. Blade 10.0 cm. long and 5.5 cm. broad to 46 cm. long and 32 cm. broad, elongate ovate-triangular or rhomboid, once pinnate or bipinnate, rarely tripinnate, light green, the pinnae at a broad angle to the rachis or ascending, entire or divided into 3–18 segments, long stalked, the pinna-rachises up to 10 cm. long, usually flexuous. Segments 0.5 cm. long and 0.5



8A. Distribution of *Pellaea sagittata* var. *cordata*, 8B. var. *sagittata*.

cm. broad to 5.5 cm. long and 2.75 cm. broad, rotundate-cordate to oblong-sagittate, entire, herbaceous to subcoriaceous, glabrous or puberulent on the under surface and along the margin of the upper surface, veins evident, the border white or lutescent, crenulate, the apex obtuse. Sporangia with short stalks rarely exceeding one half the capsule length, the annulus occasionally irregular-oblique or with a cluster of cells at the apex of the capsule. Spores 64 or 32 per sporangium, ellipsoidal or tetrahedral-globose, yellow or light brown, the exospore with sparse, prominent rugae.

The varieties of *P. sagittata—cordata* and *sagittata*—are appropriately named from the form of the segments but are often confused and the matter is further complicated by mixtures of the two under the same number as in the abundant Pringle collections. In addition to the differences in segment form they can be distinguished on several other characters, most easily seen in living plants, as noted in the discussions of the varieties.

The range of the species is extended from Mexico southward to Bolivia by the apogamous variety. In the highlands of central Mexico both types occur in abundance and appear equally vigorous. The apogamous plants do not appear to have any advantage over the normal type except that they, of course, would not require the moisture necessary for fertilization. The two varieties usually grow a few miles apart in colonies of a few to 25 independent plants but on calcareous soils near Cuernavaca, Mexico, I have found them growing together. Preliminary cytology work indicates that the apogamous var. *sagittata* is a triploid with 87 chromosomes. The collections which have been cytologically examined by Dr. Britton are from Mexico. One near Morelia in the state of Michoacán collected by R. M. & A. F. Tryon *5153* had both n and 2n chromosome numbers of 87. Collections of var. *cordata 5147* and *5149* from El Pedregal in the Distrito Federal were both reported as probably n = 29 by Dr. Britton. It seems possible that the latter and *P. ovata*, which has both normal and apogamous strains, are the most likely parents of *P. sagittata* var. *sagittata*.

Key to Varieties

Segments rotundate-cordate; rachis and segment stalks glabrous; spores 64 per sporangium, tetrahedral-globose, 37–53 μ at broadest diameter; southern Texas southward in Mexico to Oaxaca.........8A. *P. sagittata* var. *cordata*, p. 166

Segments ovate-triangular to sagittate; rachis and segment stalks usually puberulous; spores 32 per sporangium, ellipsoidal, 53–106 μ at broadest diameter; Chihuahua, Mexico, southward to Bolivia...8B. *P. sagittata* var. *sagittata*, p. 168

8A. Pellaea sagittata var. **cordata** (Cav.) comb. nov. Fig 8A. Map 8A.

Pteris cordata Cav. Descr. Pl. 267. 1802. (Holotype: *Née*, Chapultepec, Mexico MA, Isotype: F!).

Allosorus cordatus (Cav.) Presl, Tent. Pterid. 153. 1836.

Platyloma cordata (Cav.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

Pellaea cordata (Cav.) J. Sm. Cat. Kew Ferns, 4. 1856, not Fée, 1850–52.

Nothochlaena cordata (Cav.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.
Adianthum cordifolium Sessé & Moc. Pl. Nov. Hisp. 182. 1887–90; ed. 2, 169. 1893.
Cassebeera cordata (Cav.) Farw. in Amer. Midl. Nat. 12:281. 1931.
Pellaea cardiomorpha Weath. in Journ. Arn. Arb. 24:309. 1943, based on *Pteris cordata* Cav.

Rachis and segment stalks glabrous. Blade rather lax in habit, the pinnae at broad angles to the rachis. Segments 0.5 cm. long and 0.5 cm. broad to 3.0 cm. long and 2.75 cm. broad, rotundate-cordate. Spores 35–53 μ at greatest diameter, 64 per sporangium, mostly tetrahedral-globose with trilete commissural ridges.

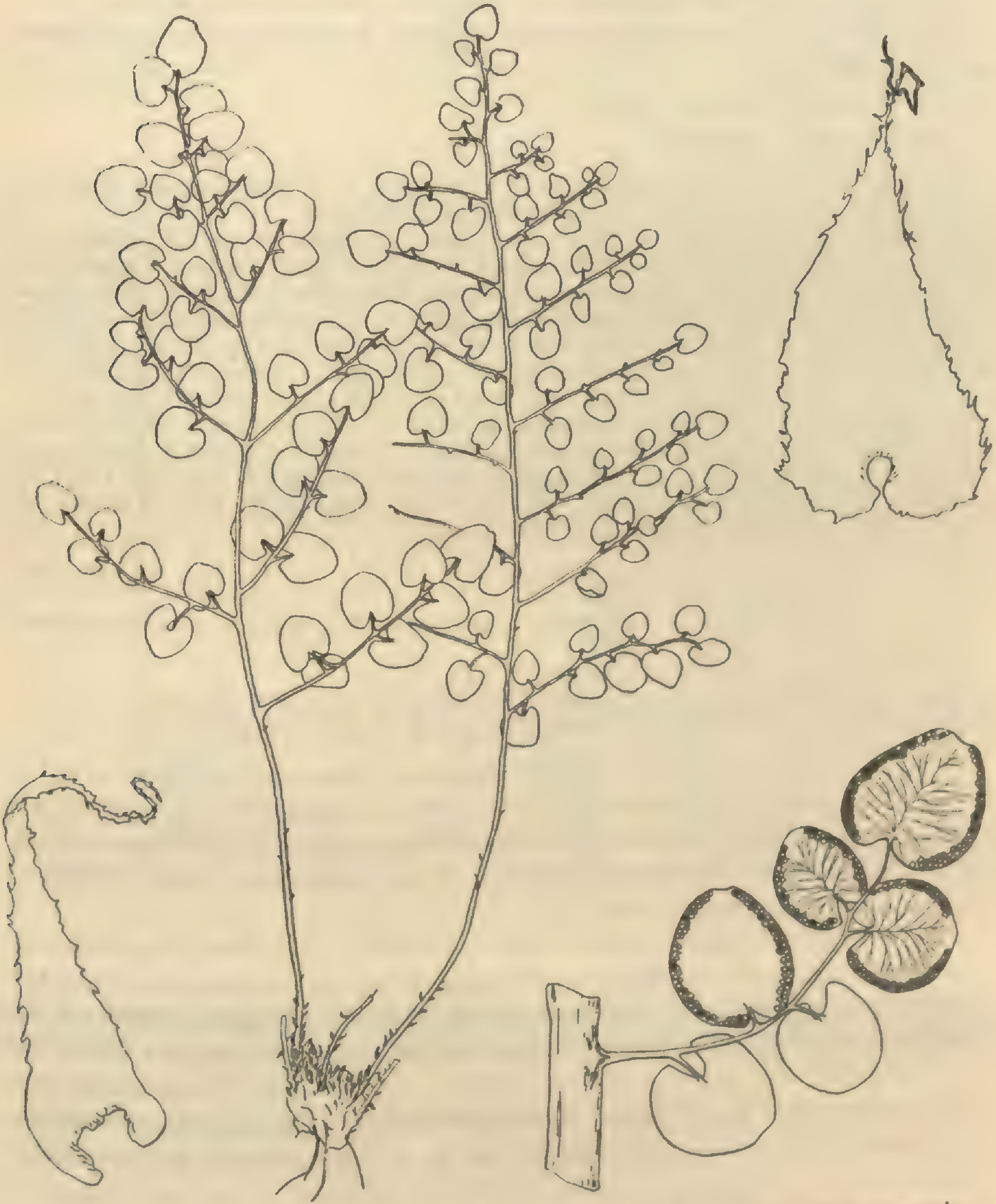


Fig. 8A. *Pellaea sagittata* var. *cordata*, plant × ½; pinna; left, rhizome scale, right, stipe scale.

Variety *cordata* is distinguished from var. *sagittata* in the lax habit of the fronds, the pinnae at broad angles to the rachis, glabrous stipes and rachises and sporangia with 64 spores, in addition to the cordate form of the segments.

Cavanilles cites Née collections from Chalma and Chapultepec, Mexico, under *Pteris cordata* and the holotype at Madrid is indicated by Christensen[29] as the Chapultepec specimen. Two fragments, one of var. *cordata* and the other of var. *sagittata* from the Née collection, on a single sheet in the Chicago Natural History Museum herbarium are labeled Chalma & Chapultepec. The larger specimen is var. *cordata* from Chapultepec and the other is var. *sagittata* from Chalma.

In open or shade, moist or dry rocks, andesitic, porphyritic, lava or limestone, at 1900–2900 m.

Southwestern Texas to Oaxaca.

Representative specimens:

United States. texas: *Hinckley 1010* (NY, US); *E. J. Palmer 34301* (GH, NY, US); *R. M. & A. F. Tryon 5081* (GH, K, MEXU, MO, U, US).

Mexico. Chapultepec, *Née* (F). chihuahua: *LeSueur 1139* (UC, GH, US); *Pringle 448* (F, GH, MEXU, MO, NY, UC, US, YU). coahuila: *Wynd & Mueller 590* (GH, MO, NY, US). distrito federal: *Matuda 18828* (US); *R. M. & A. F. Tryon 5103* (MO), *5147* (MO), *5149* (GH, MEXU, MO, US). guanajuato: *Kenoyer 1787* (US). hidalgo: *Rose & Painter 6741* (GH, NY, US); *R. M. & A. F. Tryon 5124* (GH, MEXU, MO, US). mexico: *Bourgeau 685* (GH, NY, P, US); *Lemmon 50* (F, GH, UC, US); *Rose & Painter 6825* (GH, US). michoacán: *Arsène 2970* (MEXU, MO, P, US); *C. & E. Seler 1233* (GH, US). morelos: *R. M. & A. F. Tryon 5121* (MO). nuevo león: *C. H. & M. T. Mueller 970* (F, GH, MEXU). oaxaca: *Conzatti & Gonzáles 521* (GH), *521a* (GH). puebla: *Arsène 9961* (US); *Purpus 2712a* (F, GH, NY, UC, US). querétaro: *J. N. & J. S. Rose 11196* (NY, US). san luis potosí: *Parry & Palmer 980* (F, MO, NY, US, YU). zacatecas: *Lloyd 247* (US).

8B. Pellaea sagittata var. **sagittata**. Fig. 8B. Map 8B.

Pteris sagittata Cav. Descr. Pl. 267. 1802. (Holotype: *Née*, Cerro de Guadeloupe, Mexico MA).
Allosorus sagittatus (Cav.) Presl, Tent. Pterid. 153. 1836.
Platyloma sagittata (Cav.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.
Pellaea cordata f. *sagittata* (Cav.) Davenp. in Bot. Gaz. 21:261. 1896.

Rachis and segment stalks usually puberulous. Blade stiff and erect in habit, the pinnae ascending at acute angles to the rachis. Segments 0.5 cm. long and 0.5 cm. broad to 5.5 cm. long and 2.0 cm. broad, ovate-triangular to oblong-sagittate. Spores 53–106 μ at the greatest diameter, 32 per sporangium, mostly ellipsoidal with monolete commissural ridge.

Variety *sagittata* is distinguished from var. *cordata* in the erect, rigid habit of the fronds, the pinnae ascending at acute angles to the rachis, puberulous stipes and rachises and sporangia with 32 spores, in addition to the sagittate form of the segments. The tawny scales of the base of the stipes and buds are fewer and smaller in var. *sagittata* than in var. *cordata*. The presence of pubescence, particularly on the rachises, appears to be correlated with the apogamous condition. In *P. ovata* and *P. andromedaefolia*, as well as in this variety, it is a convenient

[29] Dansk Bot. Ark. 9:23. 1937.

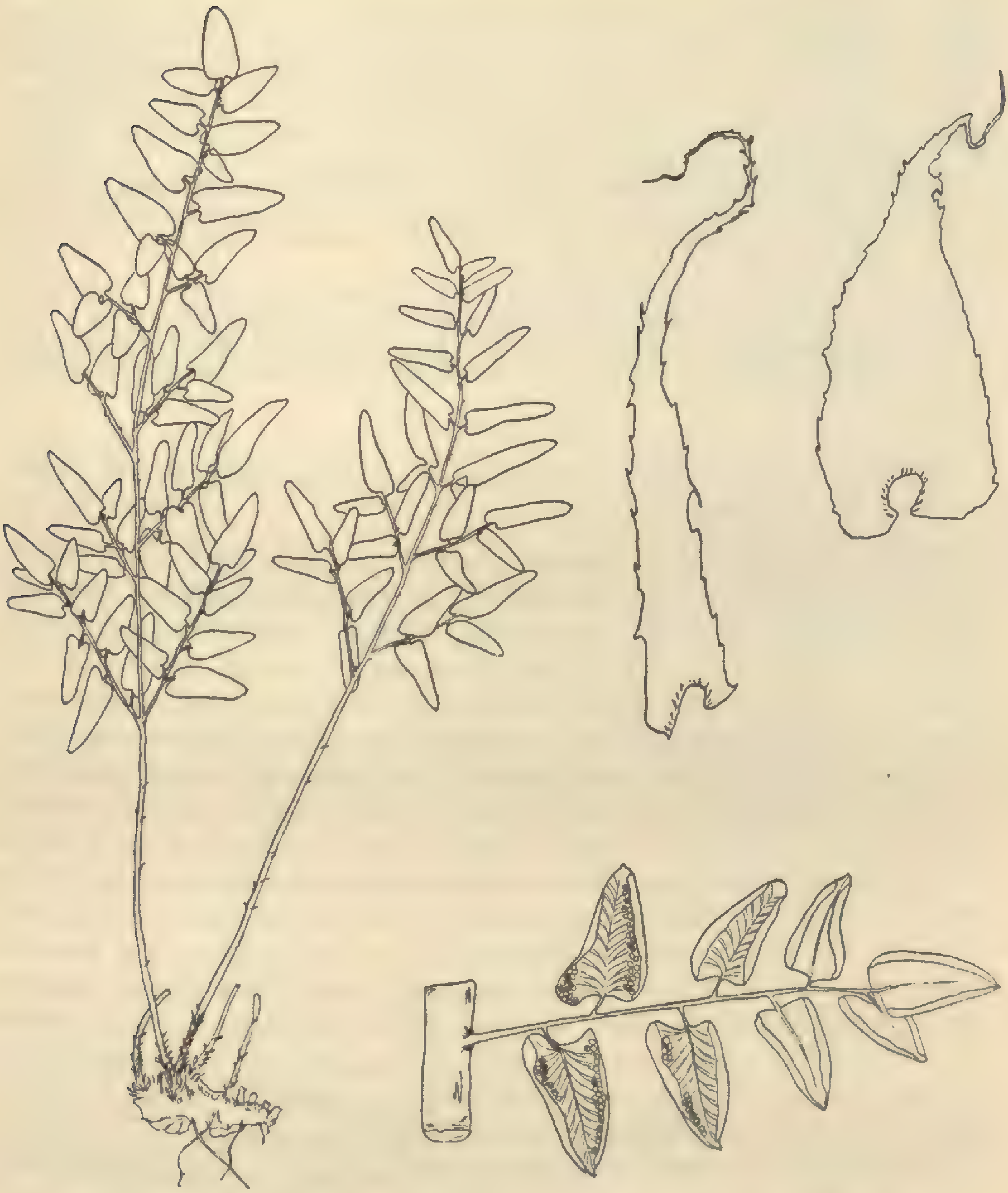


Fig. 8B. *Pellaea sagittata* var. *sagittata*, plant × ½; pinna; left, rhizome scale, right, stipe scale.

clue for detecting specimens with 32 spored sporangia and apparently apogamous.

On dry banks, in open or shade, among limestone rocks, on adobe walls or stone fences, at 1700–3000 m.

Northern Mexico to Guatemala; Colombia to Bolivia.

Representative specimens:

MEXICO. CHIAPAS: *Ghiesbreght 303* (F, GH, YU). CHIHUAHUA: *Knobloch 5940* (GH, MSC, US). DISTRITO FEDERAL: *Matuda 26234* (US). HIDALGO: *Mexia 2760* (UC).

JALISCO: *McVaugh 12974* (US). MEXICO: *Bourgeau 1163* (GH, P); *Rose et al. 9464* (F, US); *R. M. & A. F. Tryon 5138* (GH, MEXU, MO, US). MICHOACÁN: *Arsène 6546* (MEXU, MO, US); *R. M. & A. F. Tryon 5153* (MO). MORELOS: *Hitchcock & Stanford 7089* (UC); *R. M. & A. F. Tryon 5122* (MEXU, MO). OAXACA: *Conzatti & Gonzáles 428* (GH, MEXU, P); *Pringle 4887* (GH, MEXU, MO, NY, P, UC, US). PUEBLA: *Arsène 7027* (GH, MO, US). TLAXCALA: *Arsène 9971* (US). SAN LUIS POTOSÍ: *Schaffner 959* (GH, YU). ZACATECAS: *Rose 2795* (GH, US).

GUATEMALA. QUEZALTENANGO: *Skutch 805* (F, GH, US). SANTA ROSÁ: *Heyde & Lux 6282* (F, GH, MO, NY, US).

COLOMBIA. CAUCA: *Killip 6877* (GH, NY, US); *Lehmann 5710* (F, P, US). SANTANDER: *Killip & Smith 17440* (NY, US).

ECUADOR. IMBABURA: *Mexia 7428* (UC, US); *Wiggins 10272* (US). PICHINCHA: *Asplund 6297* (US); *Couthouy 39* (GH, YU); *Mille 130* (GH, MO, US).

PERU. APURIMAC: *Stork et al. 10648* (F, UC). CUZCO: *Herrera 1195* (F, US); *Vargas 11049* (F, UC). HUANCAVELICA: *Tovar 317* (US). LIMA: *Macbride & Featherstone 422* (F, GH, US).

BOLIVIA. LA PAZ: *Mandon 1554* (GH).

9. PELLAEA NOTABILIS Maxon, in Contrib. U. S. Nat. Herb. 10:500. 1908. (Holotype: *Palmer 234* US!). Fig. 9. Map. 9.

Rhizome moderately stout, compact, decumbent, multicipital. Scales of the rhizome appressed and matted, rust colored, the young tips light tan, these and those at the base of the stipes concolorous, subulate, straight or nearly so, the margins pectinate-serrulate, the cells short rectangular or with oblique end-walls or elongate, the apex long attenuate. Fronds 12–43 cm. long, erect, straight, stiff, approximate, monomorphic, the buds pubescent. Stipe and rachis terete or elliptical, pubescent, the rachis and upper portion of the stipe straw to buff colored, the stipe base and segment stalks atropurpureous, the stipe breaking irregularly without articulation lines, the rachis straight. Blade 3.5 cm. long and 3.5 cm. broad to 23 cm. long and 14 cm. broad, deltoid or elongate-triangular, once pinnate, grayish green, the pinnae at broad angles to the rachis or somewhat ascending, entire, short stalked, without pinnae-rachises. Segments 3.0 cm. long and 0.75 cm. broad to 7 cm. long and 1 cm. broad, elongate-lanceolate, entire, subcoriaceous, glabrous, veins obscure, the border narrow, lutescent, slightly crenulate, the apex more or less mucronate. Sporangia with short stalks not exceeding the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, yellow or light brown with prominent, rugose and somewhat lacy exospore.

Although clearly unique, the position of this rare fern is intermediate between the dark and light stiped groups. It resembles *P. atropurpurea* in having concolorous scales, terete rachises and atropurpureous color at the base of the stipes and petiolules. Similarities to *P. ovata* and *P. sagittata* occur in the predominant straw color of the rachises and stipes, the prominent spore ornamentation and the pectinate-serrulate scales. The subulate form of the scales is similar to *P. ovata* and both of these species have been collected in Tamaulipas. Since there are so few collections of *P. notabilis* I searched for it at some length in the vicinity of Monterrey—but with no success. It appears to be a rare fern possibly restricted to select ecological niches which are explored with some difficulty in that region.

Fig. 9. *Pellaea notabilis*, plant × ½; pinna; rhizome scale.

Among rocks, at 320–1100 m.
Tamaulipas and Nuevo León.

Mexico. nuevo león: *Sanchez 316* (US). tamaulipas: *Bartlett 10352* (US); 1902, *Kemp* (NY); among rocks in cañon, vicinity of Victoria, alt. about 320 m., Feb. 1–April 9, 1907, *E. Palmer 234* (US); *Stanford et al. 2129* (US).

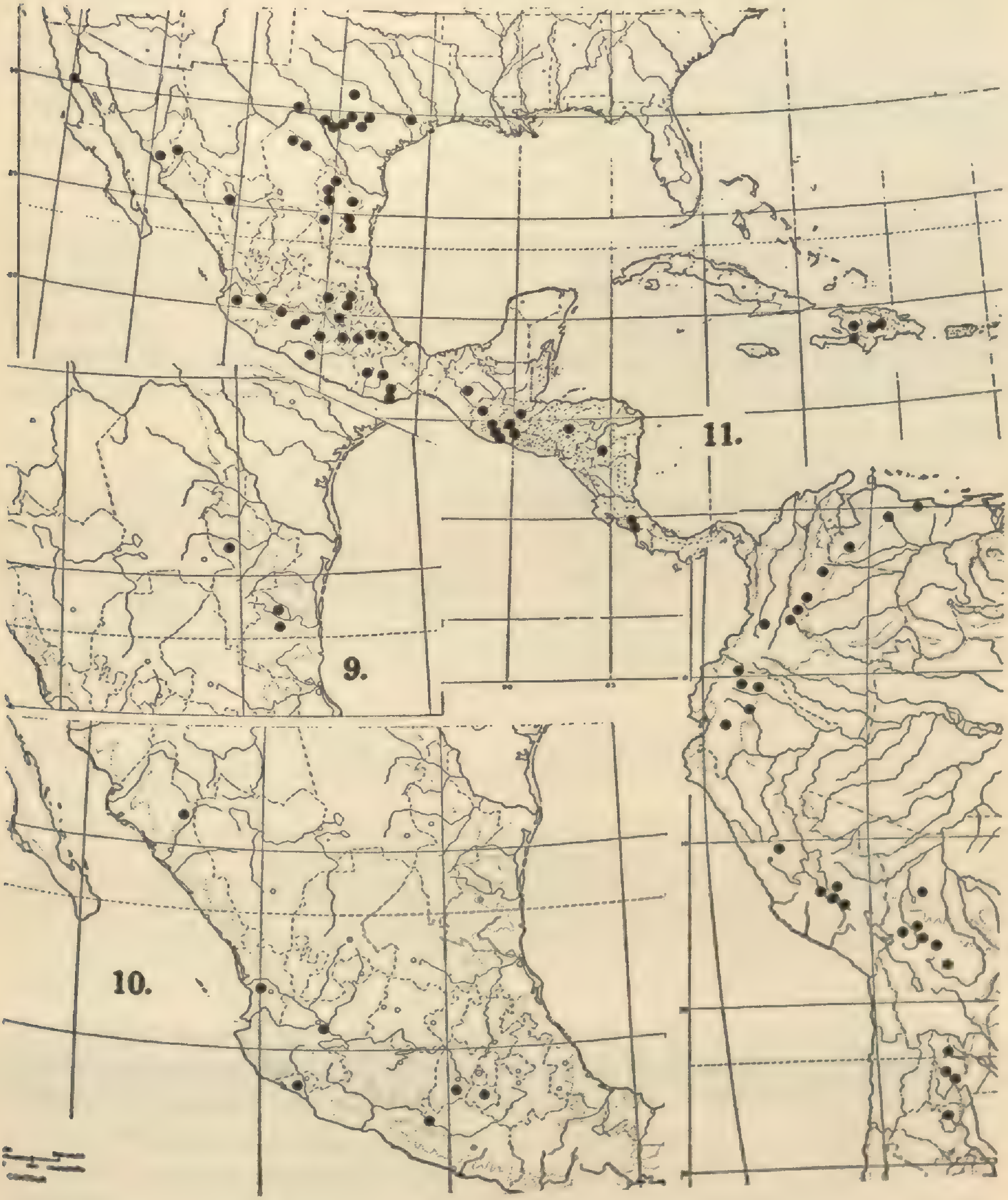
10. Pellaea pringlei Davenp. in Gard. & For. 4:555. 1891. (Holotype: *Pringle 2591* GH!, Isotypes: F! MO! US!, Paratype: *Palmer 543* US!). Fig. 10. Map 10.

Allosorus Pringlei (Davenp.) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Rhizome moderately stout, compact, multicipital, decumbent. Scales of the rhizome appressed, tan to ruddy brown, these and those of the base of the stipes concolorous, the scale base often sclerotic and adherent to the stipe, acicular, straight or nearly so, the margins entire or sparsely dentate, the cells short-rectangular or elongate with oblique end-walls, the apex long-attenuate. Fronds 6–47 cm. long, erect, straight or nearly so, approximate, the sterile fronds shorter, the buds covered with subulate scales. Stipe and rachis convex or plane on the

Fig. 10. *Pellaea Pringlei*, plant × ½; pinna; rhizome scale.

upper surface, or channeled, more or less paleaceous, the rachis and upper portion of the stipe straw-yellow or mottled, the stipe base darker, usually atropurpureous, the stipe breaking irregularly without articulation lines, the rachis straight. Blade 4.0 cm. long and 2.5 cm. broad to 20 cm. long and 13 cm. broad, elongate-triangular, once pinnate or bipinnate, bluish green, the pinnae ascending, entire or with 2–3 segments, usually long stalked, the pinna-rachises less than 0.5 cm.



9. Distribution of *Pellaea notabilis*, 10. Distribution of *Pellaea Pringlei*, 11. Distribution of *Pellaea ovata*.

long, usually absent. Segments 0.75 cm. long and 1.0 cm. broad to 4.0 cm. long and 4.5 cm. broad, deltoid-hastate or stellate, entire, ternate or with 3–5 irregular lobes, chartaceous or herbaceous, glabrous, the veins evident, the border whitish crenulate, often opaque, bluish on the upper surface. Sporangia stalks short, one fourth the capsule length, the annulus amber colored, occasionally irregular-oblique or with a cluster of cells at the apex of the capsule. Spores 64 per sporangium, tetrahedral-globose, yellow or brownish, with prominent rugose-reticulate exospore.

The complete specimens and ample number of collections of these pellaeas made by C. G. Pringle have made possible a better understanding of the group. From his carefully prepared specimens one receives the impression that he admired these ferns. It is appropriate that this attractive species bears his name for the original as well as the most complete suites of specimens are his. It is uncommon and few others have collected it.

The stipes are largely straw colored, the pinnae star-shaped and bluish green. Some specimens are irregularly lobed rather than stellate and have incompletely formed spores. It is possible that the species may be a hybrid of *P. ternifolia* and *P. ovata* although it has distinctive acicular and largely concolorous rhizome scales. It occurs on moist limestone along the banks of streams partially within the ranges, but much more restricted, than those two species.

Uncommon, on wet calcareous banks, at 1000–2200 m.

Sinaloa south to Guerrero and Morelos.

Representative specimens:

MEXICO. COLIMA: *Reko 4846* (US). GUERRERO: *Hinton 9475* (F, NY, US). JALISCO: Río Blanco, June–Oct. 1886, *Palmer 543* (US, YU); Cool mossy banks near Guadalajara, Oct. 19, 1889, *Pringle 2591* (F, GH, MEXU, NY, P, US, YU). MEXICO: *Hinton 1537* (GH, MEXU), *4227* (GH, NY). MORELOS: *Pringle 7949* (F, GH, MO, NY, US); *Sanchez 97* (US). NAYARIT: *Mexia 709* (US). SINALOA: *Gentry 6523* (GH, MO).

11. PELLAEA OVATA (Desv.) Weatherby, in Contr. Gray Herb. 114:34. 1936. Fig. 11. Map 11.

Pteris ovata Desv. in Mém. Soc. Linn. Paris (Prodrome de la famille des Fougères) 6:301. 1827. (Holotype: Peru, Herb. Desvaux P!, Photo: GH! UC!).
Pteris flexuosa Kaulf. ex Schlect. & Cham. in Linnaea 5:614. 1830, excl. synon. (Holotype: *Schiede & Deppe*, Aug. 1828, near Jalapa, Mexico, B).
Allosorus flexuosus (Kaulf. ex Schlect. & Cham.) Kze. in Linnaea 13:136. 1839.
Pellaea flexuosa (Kaulf. ex Schlect. & Cham.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841.
Platyloma flexuosa (Kaulf. ex Schlect. & Cham.) J. Sm. in Bot. Mag. 72: Comp. 21. 1846.

Rhizome slender, cord-like, dichotomously branched, creeping or compact and enveloped by matted roots. Scales of the rhizome appressed, tan to dark brown, these and those at the base of the stipes bicolorous, elongate, lanceolate-triangular, cordate, the sclerotic central portion lustrous (old scales sclerotic except for a narrow margin), straight or somewhat falcate, the margins pectinate to erose-serrulate, the cells short-rectangular or with oblique end-walls, the apex filiform, more or less tortuous. Fronds 10–125 cm. long, straight or frequently twining,

subscandent, approximate, monomorphic, the buds on old portions of the rhizome as well as the apex, lanate to pubescent, with a few scales. Stipe and rachis convex or plane on the upper surface, glabrous or pubescent, straw colored to ruddy brown becoming gray with age, the stipe breaking irregularly without articulation lines,

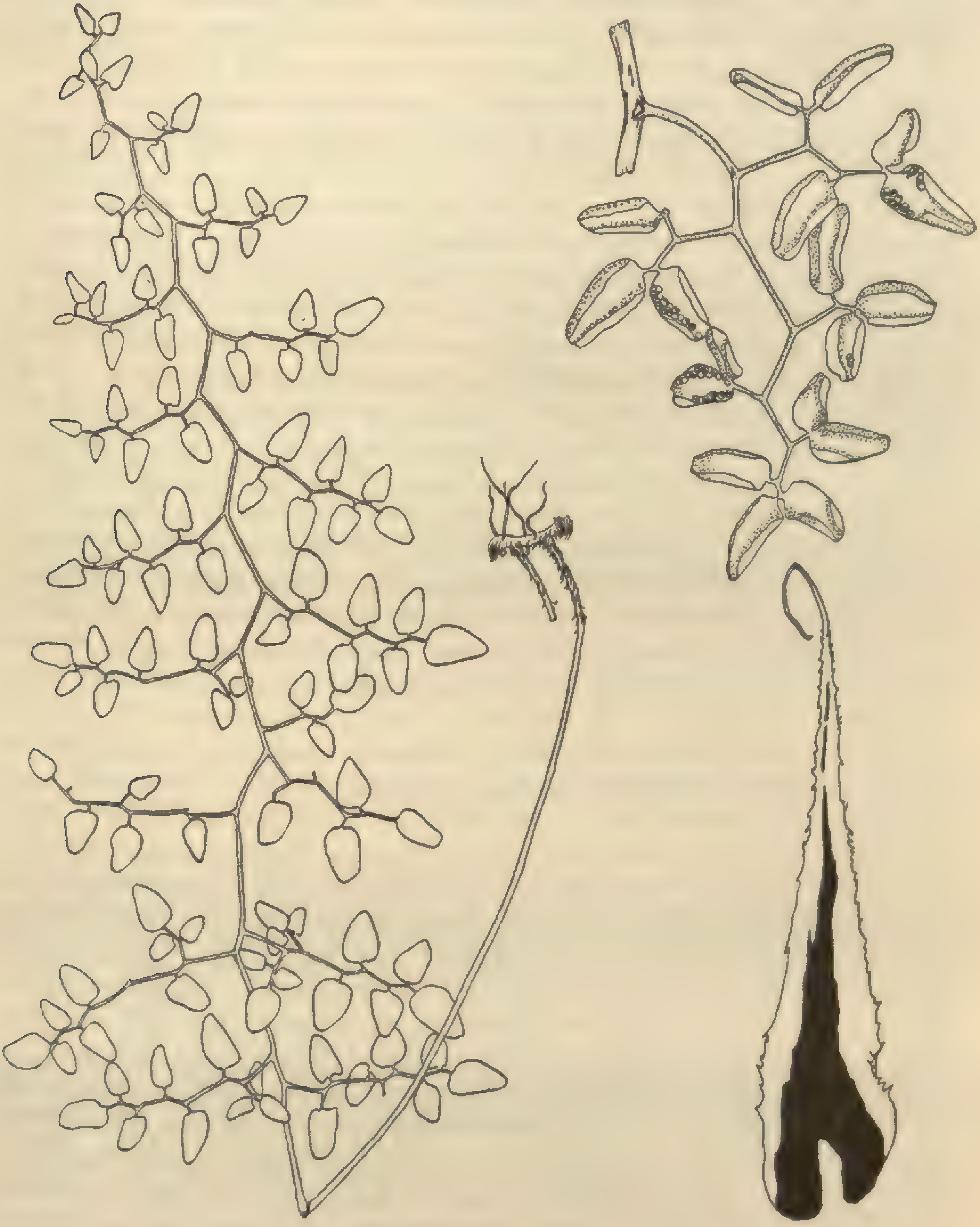


Fig. 11. *Pellaea ovata*, plant × ½; pinna; rhizome scale.

the rachis strongly flexuous. Blade 15 cm. long and 2 cm. broad to 84 cm. long and 30 cm. broad, elongate-triangular, bi- to quadripinnate usually tripinnate, clear or grayish green, the pinnae descending at broad angles to the rachis, divided into 5 or more than 60 segments, long stalked, the pinna-rachises up to 14 cm. long, strongly flexuous. Segments 0.5 cm. long and 0.3 cm. broad to 4.5 cm. long and 2.5 cm. broad, ovate-triangular, sagittate or cordate, coriaceous, glabrous or sparsely pubescent, veins obscure, the border narrow, whitish lutescent, the apex obtuse or somewhat mucronate. Sporangia with stalks as long or slightly longer than the capsule, the annulus amber colored. Spores 32, occasionally 64 per sporangium, ellipsoidal or tetrahedral-globose, yellow with prominent light brown, rugose exospore.

These are the largest plants of the section, usually subscandent and unique in the retrorse position of the pinnae and strongly flexuous rachises. The species is relatively uniform throughout most of its range from central Texas to northern Argentina and appears to be the counterpart of *P. ternifolia* in the dark stiped group. Two species, *P. intermedia* and *P. andromedaefolia* at the northern end of its range and the Chilian *P. myrtillifolia* at the southern end, are related. As in *P. glabella* and *P. sagittata* the center of origin and direction of migration of the species can be determined by the spore number. In southern Texas and adjacent Mexico the specimens are 64 spored and produce the normal type of prothallia. A collection of R. M. & A. F. Tryon from Marble Falls, Texas, was reported by Dr. Britton to have a chromosome count of $n = 29$. South of this area extending to northern Argentina and in the Caribbean region the specimens are 32 spored and apogamous and evidently account for the general uniformity of the species.

Subscandent, in open sun, brushy savanna, among limestone rocks, on shaded banks, in oak forest, or growing on adobe walls, stone fences or crotches of trees, at 800–2850 m.

Southern Texas southward in Mexico and Central America to Nicaragua; Hispaniola; Venezuela southward to northern Argentina.

Representative specimens:

United States. texas: *Correll 15230* (MO); *E. Palmer 1428* (GH, MO, US, YU); *Reverchon 1628* (F, GH, MO, US); *R. M. & A. F. Tryon 5029* (GH, K, MEXU, MO, US).

Mexico. baja california: *Lemmon 145* (US). chiapas: *Ghiesbreght 204* (GH, US); *Little & Sharp 9907* (US). chihuahua: *Gentry 1538* (F, GH, MO, UC). coahuila: *Wynd & Mueller 318* (GH, MO, US). distrito federal: *Lyonnet 861* (GH, MO, NY, US). durango: *Ortega 5313* (US). guanajuato: 1880, *Duges* (NY). guerrero: *Hinton 11305* (F, GH, MO, US). hidalgo: *Chase 7217* (F, MO). jalisco: Nov. 28, 1883, *Pringle* (F, UC), *5408* (MO, US). mexico: *Hinton 7206* (F, MO); *R. M. & A. F. Tryon 5134* (GH, K, MEXU, MO, US). michoacán: *Arsène 3645* (MEXU, US), *9985* (GH, MO, US). morelos: *Rose et al. 10193* (US). nuevo león: *C. H. & M. T. Mueller 1130* (F, GH). oaxaca: *Conzatti & Makrinius 3030* (MEXU, US); *Pringle 5951* (F, GH). puebla: *Arsène 1477* (US); *Copeland 108* (MEXU, P, UC). querétaro: *J. N. & J. S. Rose 11195* (US). san luis potosí: *Schaffner 53* (P), *958* (GH, YU); *R. M. & A. F. Tryon 5154* (MO). sonora: *Rose et al. 13113* (US). tamaulipas: *Bartlett 10313* (US). veracruz: *Bourgeau 3067* (GH, NY, P, UC, US, YU); *Seaton* 39 (F, GH, NY, US).

Guatemala: 1862, *Godman & Salvin* (BM); *Hatch & Wilson 330* (UC, US); *Standley 77095* (F, US); *Steyermark 47282* (F, US).

HONDURAS: *Standley 56496* (F, US).
NICARAGUA: *Standley 9721* (F), *10192* (F).
COSTA RICA: *Brade 199* (NY, UC), *16403* (P, US); *Valerio 169* (US).
HISPANIOLA. HAITI: *Ekman H6153* (NY, US); *Leonard 4804* (GH, NY, UC). DOMINICAN REPUBLIC: *R. A. & E. S. Howard 8823* (GH, MO, NY, US).
VENEZUELA. *Eggers 13417* (F, US); *Pittier 7040* (GH, US). DISTRITO FEDERAL: *Jahn 230* (US); 1929, *Vogl* (S-PA, UC). MÉRIDA: *Fendler 89* (GH, MO, NY); *Jahn 1082* (US).
COLOMBIA. VALLE: *Cuatrecasas 20467* (F, US); *Killip & Smith 16382* (GH, NY, US), *19090* (F, GH, US).
ECUADOR. Sept. 1918, *Mille* (S-PA), *131* (GH, US). AZUAY: *Haught 3346* (GH, US). CHIMBORAZO: *Camp 3167* (MO, US). IMBABURA: *Mexia 7404* (F, UC, US); *Wiggins 10270* (US). PICHINCHA: *Asplund 6572* (US); *Firmin 236* (NY, US).
PERU. APURÍMAC: *Herrera 1497* (F, GH); *Stork & Horton 10712* (F, UC). CUZCO: *Cook & Gilbert 254* (US); *Soukup 754* (F, GH); *Vargas 1051* (GH, MO). HUÁNUCO: *Sawada P108* (F). LORETO: *Macbride 3142* (F, US).
BOLIVIA. April 1892, *Kuntze* (NY); *Rusby 142* (NY, US). COCHABAMBA: *Cardenas 3313* (F), *4798* (US); *Janssen 70* (S-PA).
ARGENTINA. CATAMARCA: Oct. 1910, *Castillon* (GH). JUJUY: Aug. 1925, *Cockerell* (US); *Eyerdam & Beetle 22417* (UC). TUCUMÁN: *Borsini 13* (GH); *Venturi 10367* (GH, MO, S-PA, US).

12. PELLAEA INTERMEDIA Mett. ex Kuhn, in Linnaea 38:84. 1869. (Holotype: "Mexico, Herb. Fournier" B?). Fig. 12. Map 12.

Pellaea intermedia var. *pubescens* Mett. ex Kuhn, loc. cit. 1869. (Holotype: *Wright* Field no. *1190*, Label no *825* B, Isotypes: GH! MO!).
Cassebeera intermedia (Mett. ex Kuhn) Farw. in Amer. Midl. Nat. 12:281. 1931.
Pellaea intermedia f. *pubescens* (Mett. ex Kuhn) Broun, Ind. N. Amer. Ferns, 132. 1938.

Rhizome slender, cord-like, dichotomously branched, long-creeping. Scales of the rhizome appressed, brownish, these and those of the base of the stipes bicolorous, elongate lanceolate-triangular, usually cordate, the sclerotic central portion usually lustrous (old scales sclerotic except for a narrow margin), straight or nearly so, the margins pectinate-serrulate, the cells short rectangular or with oblique end-walls, the apex filiform. Fronds 10 to more than 65 cm. long (largest specimens examined were incomplete), erect, straight and stiff, distant, monomorphic, the buds pubescent and with a few scales on the older portions of the rhizome as well as at the apex. Stipe and rachis convex or plane on the upper surface, more or less puberulent, straw colored to ruddy brown, becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous. Blade 8.0 cm. long and 3.5 cm. broad to 25 cm. long and 18 cm. broad, elongate-triangular, once pinnate to tripinnate, usually bipinnate, clear or grayish green, the pinnae at a broad angle to the rachis or slightly ascending, divided into 3–25 segments, long stalked, the pinna-rachises up to 10 cm. long, usually straight. Segments 0.5 cm. long and 0.3 cm. broad to 2.0 cm. long and 1.8 cm. broad, ovate to ellipsoidal, entire or ternate, coriaceous, glabrous, the veins obscure the borders narrow, whitish, the apex obtuse or somewhat mucronate. Sporangia with stalks as long or longer than the capsule, the annulus amber colored. Spores 32 or occasionally 64 per sporangium, ellipsoidal or tetrahedral-globose, yellowish with prominent tan or light brown, rugose exospore.

The choice of the name *P. intermedia* by Mettenius is of interest for he considered the species to be a hybrid between *P. sagittata* and *P. ovata*. This observation of the occurrence of a hybrid in nature is exceptional for that time. The closest relationship of *P. intermedia* as expressed in the form of the rhizome and leaves appears to be with *P. andromedaefolia* and *P. ovata*.

Although the type of *P. intermedia* was not examined the pubescent variety is not maintained. All of the collections seen were somewhat pubescent and the

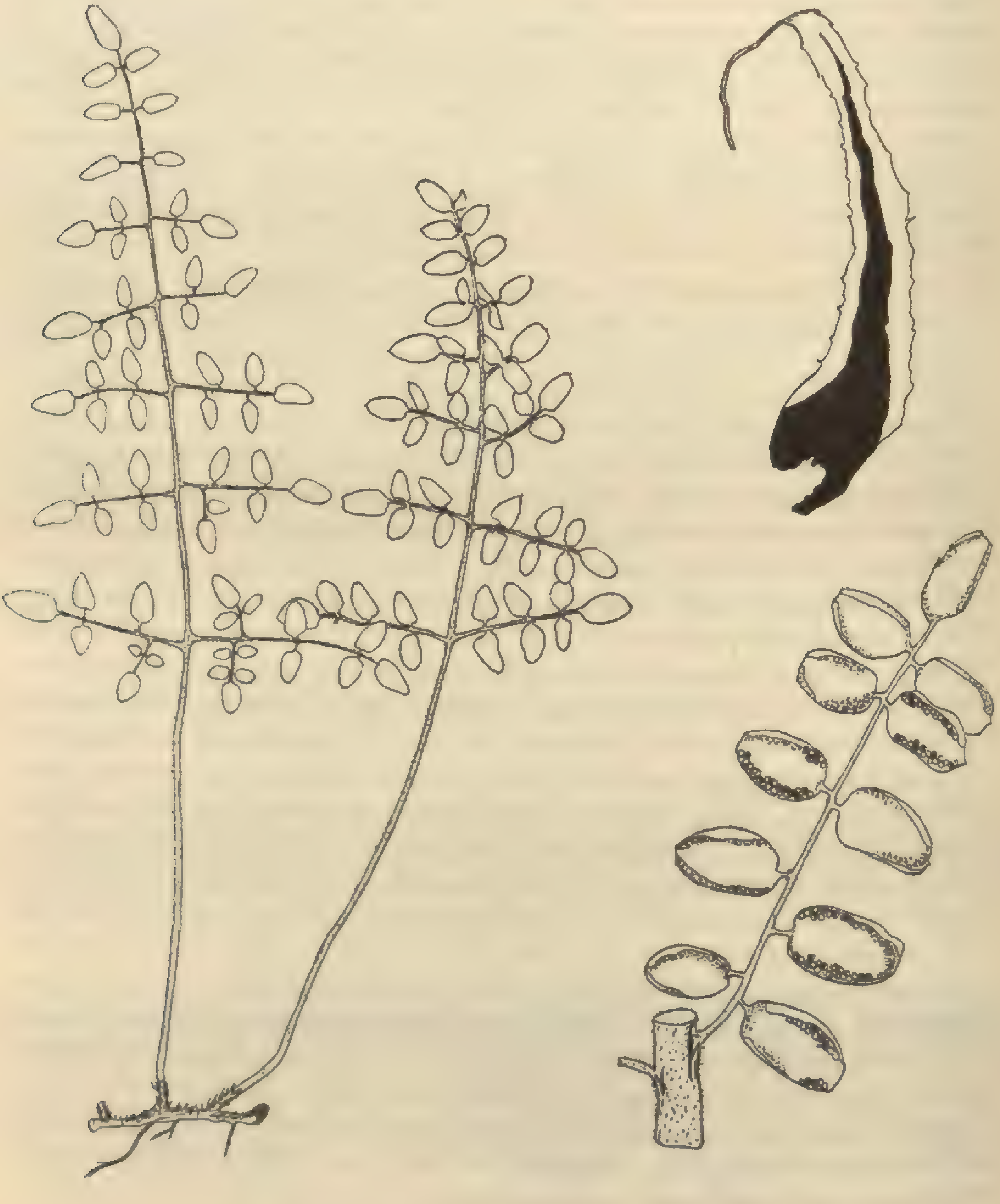


Fig. 12. *Pellaea intermedia*, plant × ½; pinna; rhizome scale.

plants seem to become less so with age. Even though the type might be completely glabrous the single specimen would not validate the recognition of two varieties.

On shaded hillsides in oak humus or among limestone, porphyritic, or sandstone rocks, at 650–2400 m.

Trans-Pecos Texas to Arizona southward in Mexico to Zacatecas.

Representative specimens:

UNITED STATES. TEXAS: *Mueller 8260* (GH, MO, NY, US); *E. J. Palmer 34078* (MO, NY); *R. M. & A. F. Tryon 5040* (GH, K, MO, US); *C. Wright 825 (1190)* (GH, MO). NEW MEXICO: *Metcalfe 1177* (F, GH, US); Oct. 5, 1880, *Rusby* (F, GH, MO, NY, US, YU); Aug. 16, 1895, *Wooton* (GH, YU). ARIZONA: *Blumer 1528* (F, GH, MO, NY, US); *Goodding 770* (GH, US); Nov. 1, 1880, *Greene* (F, NY); *Rothrock 494* (F, US), *674* (GH).

MEXICO. CHIHUAHUA: *Pringle 461* (NY, US), *930* (MEXU, MO, NY, US). COAHUILA: *Hinton 16700* (US); *Johnston & Mueller 642* (GH), *859* (GH); *E. Palmer 1426* (GH, US, YU), *1427* (GH, MO, US, YU); *Stanford et al. 161* (GH, MEXU, NY, US), *354* (GH, MO, NY, US). NUEVO LEÓN: *Mueller 1079* (GH); *Taylor 84* (US). SONORA: *White 330* (GH), *4743* (GH). ZACATECAS: *Lloyd & Kirkwood 22* (MO), *135* (GH).

13. PELLAEA ANDROMEDAEFOLIA (Kaulf.) Fée, Gen. Fil. 129. 1850–52.
Fig. 13. Map 13.

Pteris andromedaefolia Kaulf. Enum. Fil. 188. 1824. (Holotype: *Chamisso*, Calif. P!, Photo: GH! US!).

Allosorus andromedaefolius (Kaulf.) Kze. in Linnaea 9:56. 1834.

Platyloma andromedaefolia (Kaulf.) J. Sm. in Journ. Bot. ed. W. J. Hooker 4:160. 1841.

Crypteris divaricata Nutt. ex Hook. Sp. Fil. 2:149. 1858, in synon.

Crypteris pubescens Nutt. ex Hook. loc. cit. 1858, in synon.

Nothochlaena andromedaefolia (Kaulf.) Keyserl. Polyp. Cyath. Herb. Bung. 29. 1873.

Pellaea andromedaefolia var. *pubescens* D.C. Eaton, Ferns N. Amer. 1:205. 1878, not properly of Baker, Syn. Fil. 150. 1868, which lists "*β C. pubescens*".

Pellaea andromedaefolia var. *rubens* D.C. Eaton, in Bull. Torr. Bot. Club 6:360. 1879. (Holotype: *Mrs. S. P. Cooper*, Santa Barbara, Calif. YU!).

Pellaea rafaelensis Moxley, in Amer. Fern Journ. 5:107. 1915. (Holotype: *Moxley 214* LA, Photo: F! US!).

Cassebeera andromedaefolia (Kaulf.) Farw. in Amer. Midl. Nat. 12:280. 1931.

Cassebeera andromedaefolia var. *gracilis* Summers ex Farw. loc. cit. 281. 1931. (Holotype: *Mrs. R. W. Summers*, San Luis Obispo Co., Calif. MICH!).

Cassebeera andromedaefolia var. *pubescens* Farw. loc. cit. 281. 1931, nom. nud., based on "*Cheilanthes pubescens* Nutt."; evidently an attempted transfer of var. *pubescens* D.C. Eaton.

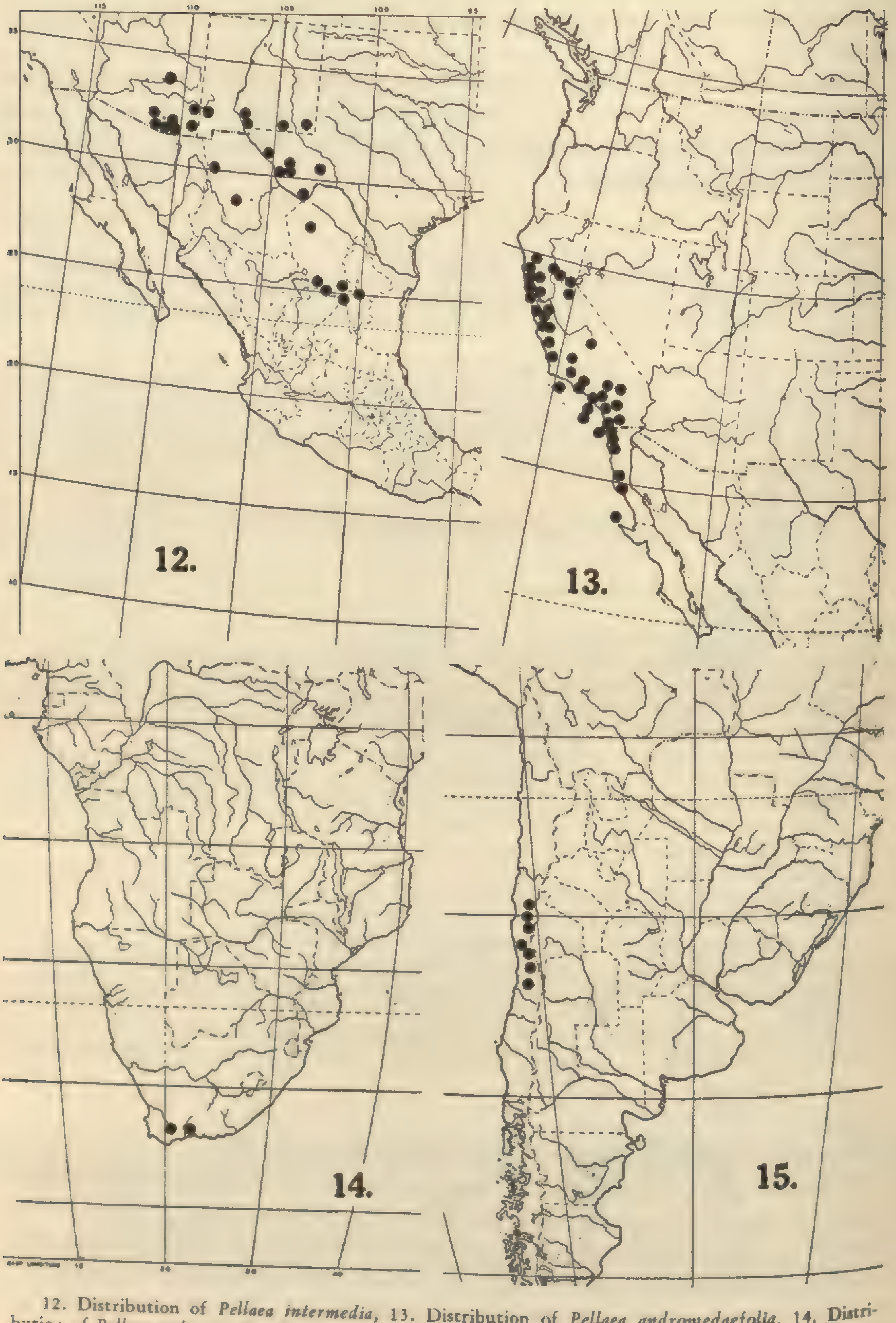
Cassebeera andromedaefolia var. *rubens* (D. C. Eaton) Farw. loc. cit. 281. 1931.

Cheilanthes pubescens Nutt. ex Farw. loc. cit. 281. 1931, in synon., apparently an error for "C[*rypteris*] *pubescens*" Nutt.

Pellaea andromedaefolia f. *gracilis* (Summers ex Farw.) Broun, Ind. N. Amer. Ferns 129. 1938.

Pellaea andromedaefolia f. *pubescens* (Eaton) Broun, loc. cit. 1938.

Rhizome slender, cord-like, dichotomously branched, long-creeping, rarely compact. Scales of the rhizome appressed, ruddy brown, these and those of the base of the stipes bicolorous, elongate lanceolate-triangular, usually cordate, the sclerotic central portion lustrous (old scales sclerotic except for a narrow margin), straight or nearly so, the margins pectinate-serrulate, the cells short-rectangular or



12. Distribution of *Pellaea intermedia*, 13. Distribution of *Pellaea andromedaefolia*, 14. Distribution of *Pellaea rufa*, 15. Distribution of *Pellaea myrtillifolia*.

elongate with oblique end-walls, the apex filiform. Fronds 10–60 cm. long, erect, straight or nearly so, distant, rarely approximate, monomorphic, the buds paleaceous on older portions of the rhizome as well as the apex. Stipe and rachis convex or plane on the upper surface, glabrous, pubescent or paleaceous, straw colored to ruddy brown becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or somewhat flexuous. Blade 6 cm. long and

Fig. 13. *Pellaea andromedaefolia*, plant × ½; pinna; rhizome scale.

3 cm. broad to 40 cm. long and 20 cm. broad, elongate-triangular, rhomboid or deltoid, bi- to quadripinnate, usually tripinnate, clear green or occasionally reddish, the pinnae usually ascending at a broad angle to the rachis, divided into 8 to more than 50 segments, long stalked, the pinna-rachises up to 14 cm. long, usually straight. Segments 0.2 cm. long and 0.1 cm. broad to 1.8 cm. long and 1.2 cm. broad, ellipsoidal or ovate, retuse, entire or ternate, herbaceous, glabrous or pubescent, veins evident, the borders narrow, whitish lutescent. Sporangia with short stalks usually less than one half the capsule length, the annulus amber colored. Spores 64 or 32 per sporangium, tetrahedral-globose or ellipsoidal, yellowish, with prominent tan or light brown, rugose exospore.

This species is closely allied to *P. intermedia*, *P. ovata* and an African species, *P. rufa*. They form a unique group characterized by reddish segments and the slender, dichotomously branching rhizome. A Chilian species is related to these on the form and color of the leaves and the form of the rhizome scales. The geographic pattern of the species of this group in the Americas is similar to that of other members of the section having a Cordilleran range. The alliance with *P. rufa* in the Karroo of South Africa, however, forms the only apparent link between the two main geographical centers of the genus *Pellaea*.

Most collections of *P. andromedaefolia* are glabrous and have 64-spored sporangia but plants from the southern part of the range are pubescent and have 32-spored sporangia. Both the 64 and 32 spored types have migrated to the coastal islands from the adjacent mainland. Cedrus Island off Baja California has the 32-spored plants while collections from more northerly islands, as Santa Catalina, Santa Cruz and San Clemente off the California coast, have 64 spores. The species is reported from southern Oregon on the basis of a single Howell collection from Roseburg, Douglas County. Since this collection is out of range and the spore number is not consistent with specimens from northern California the validity of the label may be questioned.

In dry, rocky ravines or ledges or along moist, shaded stream banks, at 60–1000 m.

California and Baja California.

Representative specimens.

UNITED STATES. CALIFORNIA: *Abrams 3121* (GH, MO, NY, P, US); *Abrams & McGregor 30* (GH, NY, US); *Abrams & Wiggins 350* (F, GH); Santa Barbara, *Mrs. S. P. Cooper* (YU); *Copeland 2750* (GH, MO, NY); *Eastwood 6378* (GH, NY, US); *Fosberg R83* (F, MO, NY), *676* (F, MO); *Grant 918* (F, GH, MO, US); *Hansen 656* (MO, P, US); *Heller 4998* (US), *9014* (US); *M. E. Jones 3227* (MO, NY, UC, US); *Meyer 1371* (GH, MO); *Nuttall 90* (F, US), *346* (F, US); *E. Palmer 427* (F, GH, MO, NY); *S. B. & W. F. Parish 513* (F, US); San Luis Obispo Co., *Mrs. R. W. Summers* (MICH); *Torrey 595a* (GH, NY); *R. M. & A. F. Tryon 5064* (MO); *Wiegand & Upton 2954a* (F, MO, NY).

MEXICO. BAJA CALIFORNIA: April 16, 1936, *Epling & Stewart* (NY, US); *E. Palmer 730* (NY, P, US), *749* (NY, US); *Wiggins 5152* (US), *9967* (US).

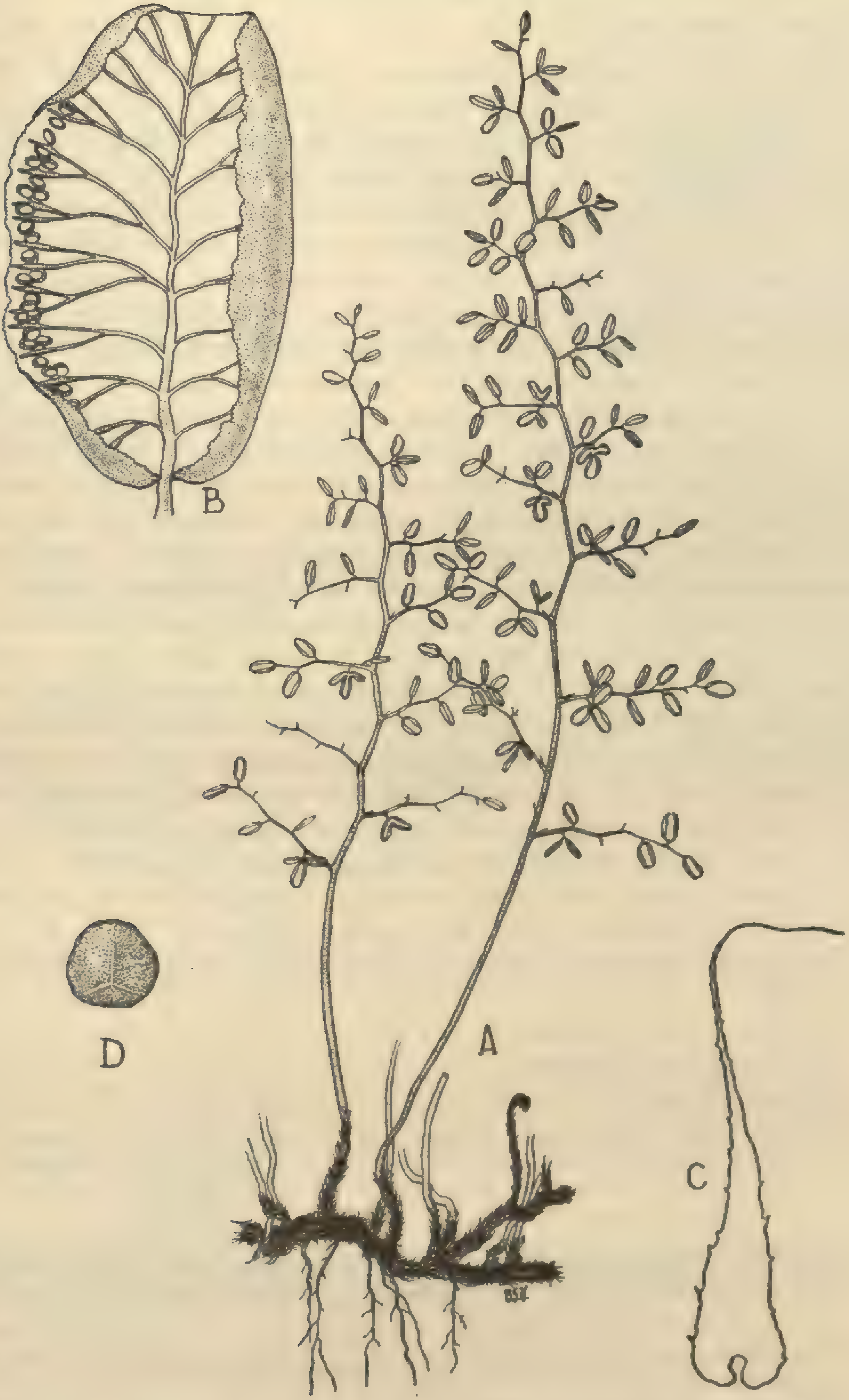


Fig. 14. *Pellaea rufa*, A, plant × ¾; B, segment with vein-ends exposed; C, rhizome scale: D, spore.

14. PELLAEA RUFA A. F. Tryon, Ann. Mo. Bot. Gard. 42:101. 1955. (Type: *Compton 16402* US!). Fig. 14. Map 14.

Rhizome slender, cord-like, dichotomously branched, long creeping. Scales of the rhizome, appressed, ruddy tan, these and those of the base of the stipes concolorous, elongate, lanceolate-triangular, cordate, the margins sparsely dentate, the cells short-rectangular or elongate with oblique end-walls, the apex filiform. Fronds 12-40 cm. long, bent or straight, approximate, monomorphic, the buds paleaceous. Stipe and rachis convex or plane on the upper surface, nearly glabrous, ruddy tan to red becoming darker and gray with age, the stipe breaking irregularly without articulation lines, the upper portion of the rachis usually flexuous. Blade 10 cm. long and 2 cm. broad to 25 cm. long and 7 cm. broad, elongate-triangular, bi- to tripinnate, the pinnae ascending at a broad angle to the rachis, divided into 6 to 15 segments, long stalked, the pinna-rachises up to 4 cm. long, somewhat flexuous. Segments 0.3 cm. long and 0.2 cm. broad to 1.0 cm. long and 0.6 cm. broad, elliptical or oval or a few ternate, retuse, coriaceous, the veins immersed and obscure, glabrous, the border lutescent, crenulate. Sporangia with short stalks less than one-fourth the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, pale yellowish brown, with smooth exospore.

This species forms the only link between the two main geographic centers of the genus *Pellaea* in Africa and the Americas. It is most closely allied to *P. myrtillifolia* in central Chile and to *P. andromedaefolia* and *P. intermedia* in the western United States. The Cordilleran species *P. ovata* is also related. A characteristic reddish color of the stipes, rachises and segments especially on immature fronds in these species is unique in the section. Relationships are also expressed in the elongate-triangular form and generally tripinnate division of the blade, in the elliptical, retuse form of the segments and elongate basally cordate scales. *P. rufa* has concolorous rhizome scales similar to those of *P. myrtillifolia* but has a cord-like, creeping rhizome similar to that of *P. andromedaefolia.*

The range of the species is largely within a radius of 40 miles in the vicinity of Whitehill.

In crevices on rocky hillsides, at 1000 m.

Cape Province, South Africa.

Specimens examined:

UNION OF SOUTH AFRICA. CAPE PROVINCE: Rock crevices, Ngaap, Laingsburg Dist., Nov. 6, 1944, *Compton 16402* (US), *2961* (K), *12619* (US); *Dickson*, Lady Barkly, recd. 5/75 (K); 1838, *Drège* (BM, K, MO, P); *Rodin 3342* (UC, K, MO, US); *Schelpe 4922* (MO, US), *4939* (US).

15. PELLAEA MYRTILLIFOLIA Mett. ex Kuhn in Linnaea 36:85. 1869. (Lectotype: *Pöppig*, Chile, Decbr. 1827, *(Diar. 603)* cited by Kunze, Linnaea 9:56. 1834, as *Allosorus andromedaefolius* B, Isotype: P!). Fig. 15. Map 15.

Pellaea andromedaefolia of authors not Kaulf., for example Gay, Hist. Fis. y Pol. Chile Bot. 6:493. 1853.

Allosorus andromedaefolius of authors not (Kaulf.) Kze., for example Sturm, Enum. Plant. Crypt. Vasc. Chile, 15. 1858.

Allosorus myrtillifolius (Mett. ex Kuhn) O. Ktze. Rev. Gen. Pl. 2:806. 1891.

Fig. 15. *Pellaea myrtillifolia*, plant × ½; pinna; rhizome scale.

Rhizome moderately stout to slender, compact or somewhat creeping. Scales of the rhizome spreading, tawny, ruddy brown, these and those of the base of the stipes concolorous, elongate lanceolate-triangular, cordate, the margins pectinate-serrulate with the base irregularly lobed, the cells short rectangular or elongate with oblique end-walls, the apex filiform, long attenuate. Fronds 14–50 cm. long, bent or straight, approximate, monomorphic, the buds pubescent with a few scales or nearly glabrous, evident only at the rhizome apex. Stipe and rachis convex or plane on the upper surface, sparsely pubescent, buff colored to reddish becoming gray with age, the stipe breaking irregularly without articulation lines, the rachis straight or especially the upper portion flexuous. Blade 9 cm. long and 4 cm. broad to 31 cm. long and 10 cm. broad, elongate-triangular or rhomboid, tri- or quadripinnate, clear green or reddish, the pinnae ascending, divided into 15 to more than 50 segments, long stalked, the pinna-rachises up to 8 cm. long, straight or slightly flexuous. Segments 0.2 cm. long and 0.1 cm. broad to 0.8 cm. long and 0.5 cm. broad, oval or ellipsoidal, retuse, usually ternate, coriaceous, glabrous, veins obscure, the border narrow lutescent. Sporangia with short stalks less than one fourth the capsule length, the annulus amber colored. Spores 64 per sporangium, tetrahedral-globose, yellow with prominent brown, rugose exospore.

Although endemic to Chile, the species is closely related to the group discussed under *P. rufa*. Geographically, it is closest to *P. ovata* in Peru and Argentina but morphological affinities as expressed in the structure and division of the leaves and the reddish color of the segments are closer to *P. andromedaefolia* in California.

An infusion of the plant is used in some parts of Chile to allay pain and thus the vernacular names *Coca* and *Yerba Coca* have been applied.

In rock fissures, at 1000–1400 m.

Central Chile.

Representative specimens:

CHILE. *Cumings Herb. 184* (GH, K); *Gay* (CU, GH). ACONCAGUA: *Bridges 557* (K). COQUIMBO: *Pearce* (K); *Wagenknecht 18536* (MO, UC); *Wagenknecht & Looser 4500* (GH). SANTIAGO: Dec. 7, 1923, *Behn* (F); *Claude-Joseph 632* (US), *807* (US); July 1934, *Grandjot* (MO); "Les Cruzes" *Pöppig 84* (P).

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A REVISION OF THE NORTH AMERICAN SPECIES OF *GENTIANELLA* MOENCH[1,2]

JOHN M. GILLETT

When the genus *Gentianella* was segregated from the Linnaean *Gentiana* by Moench[3] in 1794 it contained but one species, *Gentianella tetrandra* Moench (= *Gentiana campestris* L.) one of the *amarella* group of gentians. In 1796 Borckhausen[4] published independently his own genus *Gentianella* to include the fringed gentians. These attempts at segregation were generally ignored, however, until 1894 when Kusnezow[5] brought together several of the present sections to constitute his subgenus GENTIANELLA of inclusive *Gentiana*, but without revision of the included species. Since then, only in occasional floras[6] has *Gentianella* been returned to generic rank with the name usually credited to Borckhausen rather than to Moench.

Thus the fundamental taxonomy of *Gentianella* has lain more or less dormant. It is astonishing that such showy and rather familiar plants should have been neglected until now. At the present time, particularly in the Americas, very few botanists even give recognition to the genus. This situation probably is due in part to the reluctance of taxonomists to undertake the many nomenclatural transfers required. Perhaps also there has been a tendency to avoid a genus with an obviously extreme degree of variability and with a range so wide that a regional study is difficult. Nevertheless this study, which includes but three of the possibly eight sections of the genus, has been attempted in an effort both better to indicate relationships and to bring order to the nomenclature.

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[1] Based on an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Contribution No. 1518, Botany and Plant Pathology Laboratory, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

[3] Moench, C., Meth. Pl. 482. 1794.

[4] Borckhausen, M. B., in Roemer's Archiv für Botanik 1:23–32. 1796.

[5] Kusnezow, N. J., in Acta Hort. Petrop. 15:1–507. 1896–1904.

[6] cf. Schustler, Fr., in Vestnik Sjezdu Cesko Bot. v. Praze, 32–34. 1923.

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Although a natural classification ideally should be based on a study of a genus in its entirety, this is not always feasible. For practical reasons it has been necessary to select regions that provide abundant study material and opportunities to study the plants at first hand in the field. However, in order to maintain perspective, representative material for the remainder of the genus throughout its range has been examined where it has been readily available.

While *Gentianella* is not as large a genus as *Gentiana (sensu stricto)*, nevertheless the total number of described species would have been unwieldy for the time available. Gilg, in his monograph,[7] described 182 South American species.[8] The number of species within the genus is not definitely established because many of those described still are included within *Gentiana*. Too often their descriptions are inadequate, so that a decision regarding their generic position is impossible without authentic material.

For this study nearly 4000 specimens have been examined from the major herbaria of North America and Europe. In addition, opportunity was afforded to study and to collect Canadian and northern United States species in the field.

This study has been based primarily on standard herbarium techniques and on field observations in natural habitats in the provinces of Alberta, British Columbia, Manitoba, Ontario, Quebec, Saskatchewan, in the Yukon Territory, and in the states of Idaho, Indiana and Wyoming. In general, seeds of North American material have been difficult to procure, and plants were difficult to maintain in cultivation. Seed exchange provides material frequently of dubious origin or consists primarily of European and Asian perennial species of *Gentiana*. More definitive studies of *Gentianella* in the future will require better facilities for observation under cultivation.

Generic Position

Gilg,[9] who made the most recent and comprehensive survey of the family, separated the Gentianaceae[10] into two subfamilies, the Gentianoideae and the Menyanthoideae. His key to the subfamilies and tribes is based primarily on pollen characters. The morphological and anatomical differences between these two subfamilies are evidently considerable as well, and although no phylogenetic relationship with other groups has been proposed it seems possible that these are two separate, perhaps scarcely related, families.

Gilg further divided his Gentianoideae into five tribes: the Gentianeae, Rusbyantheae, Helieae, Voyrieae, and Leiphaimeae. The Gentianeae, in which we are primarily interested, he divided into the subtribes Exacinae, Erythraeinae, Chironiinae, Gentianinae and Tachiinae.

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[7] Gilg, E., in Engler's Bot. Jahrb. 54 (Beibl. 118):4–89. 1916.
[8] Only one species of true *Gentiana* (*G. prostrata* Haenke) is recorded for the Andes.
[9] Gilg, E., in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 4^2:50. 1895
[10] Dumortier, B. C., Analyse Fam. Pl. 20. 1829.

Within the subtribe Gentianinae, Gilg recognized seven genera: *Crawfurdia, Jaeschkea, Gentiana (sensu lato), Ixanthus, Pleurogyne* (= *Lomotogonium*), *Swertia*, and *Halenia*. Since that time, as indicated in the historical survey which follows, *Crawfurdia* has been united in part with *Gentiana* and in part with *Gentianella*.

Gentianella is more closely related to *Swertia, Lomatogonium*, and *Halenia* than to *Gentiana*. Two groups can clearly be distinguished on the basis of the position of nectaries: *Gentiana*, with glands at the base of the ovary; *Gentianella, Swertia, Lomatogonium*, and *Halenia*, with glands, foveae, or spurs borne on the surface of the corolla alternate with the stamens. The corolla of *Gentiana*, too, bears plicae or folds between the lobes, and the calyx has a membrane or rim extending completely around the interior of the tube. The calyx lobes, which arise from immediately below the edge of this membranaceous rim, may be foliaceous or they may be reduced to teeth. Kusnezow[11] has shown that this type of calyx has developed as an invagination of the inner epidermis of the tube. The intracalycular membrane is not consistently present in species of *Gentiana*; for example, *G. douglasiana* Bongard, a west-coast species, bears no membrane, but does exhibit corolla plicae accompanied by glands at the base of the ovary. In *Gentianella* and in the other three related genera, no such membrane exists. The small membrane that extends across the interior of the sinuses of the calyx in subgenus EUBLEPHIS (the fringed gentians) appears to be of different origin, for it is never continuous around the interior of the tube but is restricted to the sinus, and extends towards the center of the outer lobes only.

Again, in *Gentiana*, the corolla lobes have 3 principal vascular bundles, while in *Gentianella* there are 5–9. I have seen too few species of the other genera in the group to comment on this character. Borodin[12] reported calcium oxalate crystals in the leaf mesophyll of all the species of *Gentiana* (subgenus EUGENTIANA) that he examined but did not find them in the species of Kusnezow's subgenus GENTIANELLA.

Although not all species have been examined cytologically, and such information might shed new light on intergeneric and interspecific relationships, some broad evolutionary relationships may be discussed. It seems evident that *Gentiana (sensu stricto)*, quite aside from its own complexity, forms part of a separate line of evolution. A second line comprises the genera *Gentianella, Halenia, Lomatogonium* and *Swertia*. These genera are rather closely related to one another through a development series of glands to fovae, fovae accompanied by squamellae and development of the squamellae themselves, to the final development of spurs. It appears certain that *Halenia* originated from a *Swertia*-like ancestor, and differentiated by the development of spurs. Allen[13] is of the opinion that the foveate Haleniae are more primitive than the spurred ones, a point of view which seems

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[11] Kusnezow, loc. cit. 1896–1904.
[12] Borodin, J., in Trav. Soc. Imp. Nat. St. Petersb. 22:131–137. 1892. (Russian).
[13] Allen, C., in Ann. Mo. Bot. Gard. 20:135. 1933.

reasonable. *Swertia* was shown by St. John[14] to be divisible into two groups, those bearing a single fovea on each petal, and those bearing two. In his revision, he used this difference as a major key character, although it appears to be of such prime importance as to suggest two separate evolutionary lines. *Lomatogonium* shows considerable affinity to *Swertia* because of the rotate corolla and the presence of squamellae.

Chromosome data available have contributed little towards the problem of generic delimitation. Table 1 provides calculated base numbers, gametic numbers, zygotic numbers and probable level of ploidy for a number of selected species.[15,16,17] From these data we glean that more than one series may exist within a genus; that the majority of the true gentians (genus *Gentiana*) of North America are diploids on a base of 13 (§ PNEUMONANTHE and § CHONDROPHYLLA), that the European § APTERA has base numbers of 7 and 13, that the Old World § THYLACITES has a base of 9, and that § CYCLOSTIGMA has a base of 7; that the genus *Gentianella* has a base 9 in both series AMARELLA and series ARCTOPHILAE of § AMARELLA, and that subgenus EUBLEPHIS (= § CROSSOPETALUM) has two series each of 11 and 13. The diploid subgenus COMASTOMA has a base of 5 in common with the genus *Lomatogonium*.

[14] St. John, H., in Amer. Midl. Nat. 26:1–29. 1941.
[15] Rork, C., in Amer. Jour. Bot. 36:687–701. 1949.
[16] Favarger, C., in Bull. Soc. Bot. Suisse 59:62–86. 1949; 62:244–257. 1952.
[17] Löve, D., in Hereditas 39:225–235. 1953.

TABLE I*

	Calculated base number	Gametic number	Zygotic number	Probable level of ploidy	Author and year
Gentiana					
COELANTHE					
G. lutea	5 or 7	ca. 17–18			Woycicki, 1935
		21	42		Stolt, 1921
		20	40		Favarger, 1949, 1952
G. purpurea	5	20			Favarger, 1949
PNEUMONANTHE					
G. andrewsii	13	13	26	Dipl.	Rork, 1949
G. asclepiadea	11	22		Dipl.	Favarger, 1949
			44		Rork, 1949
G. cherokeensis	13	13	26	Dipl.	Rork, 1949
G. clausa	13	13	26	Dipl.	Rork, 1949
G. decora	13	13	26	Dipl.	Rork, 1949
G. gebleri	13	13		Dipl.	Sokolovskaja & Strelkova, 1938
G. linearis	13	13	26	Dipl.	Rork, 1949
G. makinoi	13		26	Dipl.	Sakai, 1934
G. pneumonanthe	13	13		Dipl.	Scheerer, 1939
G. porphyrio	13	13	26	Dipl.	Rork, 1949
G. puberula	13	13		Dipl.	Rork, 1949
G. saponaria	13	13	26	Dipl.	Rork, 1949
G. villosa	13	13	26	Dipl.	Rork, 1949
FRIGIDA					
G. frigida	13	13		Dipl.	Sokol. & Strel., 1938

TABLE I (*Continued*)

	Calculated base number	Gametic number	Zygotic number	Probable level of ploidy	Author and year
APTERA					
G. cruciata	13	26	52	Tetra.	Favarger, 1949
			52		Rork, 1949
G. daburica	13	13	26	Dipl.	Rork, 1949
G. gracilipes	13	13	26	Dipl.	Rork, 1949
G. macrophylla	7	21	42	Hexa.	Rork, 1949
G. phlogifolia	13		52	Tetra.	Rork, 1949
G. straminea	13		52	Tetra.	Rork, 1949
CHONDROPHYLLA					
G. altaica	13	13			Sokol. & Strel., 1938
THYLACITES					
G. acaulis	9		36	Tetra.	Rork, 1949
G. alpina	9	18		Tetra.	Favarger, 1949
G. clusii	9	18		Tetra.	Favarger, 1949
G. kochiana	9	18		Tetra.	Favarger, 1949
CYCLOSTIGMA					
G. nivalis	7	7		Dipl.	Favarger, 1949
G. verna	7	14		Tetra.	Favarger, 1949
Gentianella					
subg. GENTIANELLA					
sect. AMARELLA					
ser. AMARELLAE					
G. amarella	9		36	Tetra.	Favarger, 1949, 1952
					Skalinska, 1952
			36		Löve, 1953
G. campestris	9	18	36	Tetra.	Favarger, 1949
					Löve, 1953
ser. ARCTOPHILAE					
G. aurea	9		36	Tetra.	Rork, 1946; Löve, 1953
G. quinquefolia	9	18	36	Tetra.	Rork, 1949
subg. EUBLEPHIS					
G. ciliata	11	22		Tetra.	Favarger, 1949
G. detonsa	11		44	Tetra.	Löve, 1953
G. crinita	13		78	Hexa.	Rork, 1949
G. procera	13	39			Rork, 1949
			ca. 80		Denniston, 1913
subg. COMASTOMA					
G. tenella	5		10	Dipl.	Favarger, 1949
					Knaben, 1950
			10		Löve, 1953
Lomatogonium					
L. rotatum	5	5	10	Dipl.	Löve, 1953
Swertia					
S. cuspidata	9		18		Sakai, 1940
S. perennis		12			Woycicki, 1937
Frasera					
F. caroliniensis	13	39	78	Hexa.	Rork, 1949

* Interpretation of the level of ploidy is, in many cases, that of the author. For more complete information see the references cited.

Tetraploidy seems to be the rule in North American subgenus GENTIANELLA, and tetraploidy and hexaploidy the rule in subgenus EUBLEPHIS. The diploid subgenus COMASTOMA is left provisionally in *Gentianella.* Of the seventy or more genera of Gentianaceae only the herbaceous members of the north temperate zone seem to have been investigated cytologically and these in a general manner only; i.e., selected species rather than all species. Probably investigations have been dependent upon the availability of seed.

Gentiana, then should be restricted to include those plants with glands at the base of the ovary and plicae between the lobes of the corolla, whether or not an intracalycular membrane is present. *Halenia,* with its spurs and dextrorse convolution of the corolla lobes in the bud, is evidently closely related to *Gentianella* subgenus GENTIANELLA.

Late-flowering plants of *Halenia deflexa* occasionally form spurless flowers that are nearly indistinguishable from *Gentianella amarella.* Nevertheless, in spite of these occasional irregularities, *Halenia* appears to be quite a distinct group worthy of generic rank. Subgenus EUBLEPHIS of *Gentianella,* on the other hand, while distinct from subgenus GENTIANELLA in ovule arrangement, constant tetramery, calyx formation, papillose seeds, etc., has been retained at the subgeneric rank to indicate close relationship with the amarellas and for reasons of usage.

I should again emphasize that this study of the North American species of *Gentianella* includes but three of the eight sections assigned to this genus (other sections include: DASYSTEPHANA Griseb. (not Adans.), ANDICOLA Griseb., IMAICOLA Griseb., ANTARCTOPHILA Griseb., and PTERYGOCALYX Maxim.), and but a minor number of the total species involved.

The segregation of *Gentianella* roughly divides the gentians into two phylogenetically distinct and quite convenient units. To separate further the fringed group as did Yu-chuan Ma,[18] chiefly on the ovule arrangement, sets a precedent that might make it necessary at a later date to segregate sections of *Gentiana* on this character. Finally we should achieve a larger number of segregates, a larger number of nomenclatural changes, and add very little more to an understanding of the group. This understanding can best be expressed by raising or lowering the ranks of the sections without unduly disturbing the generic concepts. Within *Gentianella* it is sufficient to show that the fringed gentians are distinct from the amarellas but no more so than is *G. tenella,* and that the amarellas and arctophilas are far more closely related.

In order to illustrate the position of *Gentianella* with respect to the other genera of the Gentianinae, I have prepared a key to the genera of the subtribe, including the genus *Megacodon* H. Smith of which unfortunately no material was available to me. In this instance characters employed in the key are taken from Hemsley's original description and from his extremely fine plate.

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[18] Ma, Yu-chuan, in Acta Phytotax. 1:1–19. 1951

KEY TO THE GENERA OF THE GENTIANINAE

a. Whorl of nectary glands at the base of the ovary, never appearing upon the base of the corolla tube.
 b. Corolla without interlobal plicae; calyx tubular without an intracalycular membrane, or the sepals free.
  c. Ovary approaching a bilocular condition by a lamellate intrusion of the placentae into the locular cavity; sepals united .... *Ixanthus*
  cc. Ovary unilocular, the ovules restricted to the sutures and with an additional row between them; sepals free .... *Megacodon*
 bb. Corolla with interlobal plicae; calyx tubular, generally with an intracalycular membrane, or spathiform .... *Gentiana*
aa. Whorl of nectaries upon the base of the corolla tube alternate with the stamens.
 d. Corolla tube spurred, foveate, or fimbriate at the base.
  e. Stigmas decurrent along the carpel sutures .... *Lomatogonium*
  ee. Stigmas terminal.
   f. Corolla lobes sinistrorsely convolute in the bud, spurless, with one or two fimbriate foveae at the base of the corolla tube .... *Swertia*[19]
   ff. Corolla lobes dextrorsely convolute in the bud, each with a non-fimbriate spur at the base of the corolla tube, or rarely spurless .... *Halenia*
 dd. Corolla tube bearing glands at the base between the stamens, never spurred, foveate, nor fimbriate at the base.
  g. Stamens inserted at the middle of the corolla tube or below; corolla imbricate in the bud; seeds generally many in each capsule .... *Gentianella*
  gg. Stamens inserted at the sinus of the corolla lobes; corolla valvate in the bud; seeds few in each capsule .... *Jaeschkea*

Historical Survey

The genus *Gentianella* is a segregate of the much larger *Gentiana*; hence their histories are closely interwoven. Although rather well treated by Kusnezow[20] in the monograph of his subgenus EUGENTIANA, a review of the history up to modern times and with stress on that of *Gentianella* will assist in an understanding of the generic problems existing in this portion of the Gentianaceae today.

Gentiana is generally accredited to Tournefort[21] who used a Dioscoridean[22] name commemorating legendary King Gentius of Illyria. Ruppius[23] recognized two genera, *Gentiana* and *Gentianella*, both of which are included within the modern *Gentiana (sensu lato)*. In his 'Genera Plantarum' of 1737, Linnaeus took up Tournefort's *Gentiana*, dividing the genus into seven groups, some of which correspond to contemporary sections. Later, in his 'Species Plantarum' of 1753, he redivided *Gentiana* less successfully into three groups as follows:

1. **Corollis quinquefidis subcampaniformibus* [includes *G. lutea, G. purpurea, G. punctata, G. asclepiadea, G. pneumonanthe, G. saponaria, G. villosa, G. acaulis*].
2. ***Corollis quinquefidis infundibuliformibus* [includes *G. verna, G. bavarica, G. nivalis, G. aquatica, G. utriculosa, G. centauria, G. spicata, G. quinquefolia, G. amarella*].
3. ****Corollis non quinquefidis* [includes *G. campestris, G. ciliata, G. cruciata, G. sessilis, G. filiformis, G. perfoliata*].

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[19] No attempt is made here to distinguish between *Swertia* and *Frasera*.
[20] Kusnezow, loc. cit. 1896–1904.
[21] Tournefort, J. P., Inst. Rei Herb. 80. *t. 40.* 1700.
[22] Gunther, R. T., The Greek Herbal of Dioscorides. Oxford, 1934.
[23] Ruppius, H. B., Fl. Jen. ed. 2. 17. 1726; ed. Hall. 21. 1745.

Necker,[24] in 1790, included most of the Gentianoideae in one of his all-inclusive "genera". His "genus" *Darinyphytum* not only included most of the Gentianoideae but also a great variety of incongruous groups from a number of modern families. Within this "genus" he recognized a number of "species". Some of these, "*Pneumonanthe*", "*Anthopogon*", "*Spiragyne*", and "*Thyrophora*", are equivalent in extent to modern genera. In most cases his descriptions are so inadequate that these "species" cannot be identified readily with modern taxa. Plates published in his 'Elementa Botanica' demonstrate characters used in the diagnosis of his super-genera.

This ambiguity of description, failure to include names on which his "species" were based, and his usage of a species concept quite at variance with either modern practice or that of other authors of his day, make these names *nomina invalida.* Significantly, perusal of the 1950 International Code reveals that fifty-seven Neckerian names have been rejected for one reason or another, against six conserved and three proposed for conservation.

In 1794, Moench[25] described the genus *Gentianella,* basing it on *Gentiana campestris* L. which he renamed *Gentianella tetrandra.* No other species were assigned by him to the genus.

In 1796, Schmidt[26] divided *Gentiana* of Linnaeus into six segregate genera: *Pneumonanthe, Hippion, Chironia, Gentiana, Swertia* and *Chlora. Hippion* included sections CROSSOPETALUM Froelich, AMARELLA Griseb. and ARCTOPHILA Griseb., now included within *Gentianella.* Borckhausen,[27] in a paper following in the same publication, divided Linnaeus' genus into thirteen genera of which *Gentianella* corresponded to section CROSSOPETALUM of Froelich.

Froelich[28] monographed *Gentiana,* also in 1796, describing 47 species which he divided into four undenominated groups: COELANTHE, CALATHIANAE, ENDOTRICHAE, and CROSSOPETALAE. Many later authors have assumed these to be sections. In 1829, Bunge[29] described 80 species of *Gentiana* but maintained a classification somewhat influenced by Borckhausen. His section CROSSOPETALAE corresponded to Grisebach's CROSSOPETALUM. Endlicher[30] essentially adopted Bunge's system in his 'Genera Plantarum' and maintained section CROSSOPETALUM Froel.

Grisebach's monographic study of the Gentianaceae[31] is one of the landmark works of the family. His genus *Gentiana* contains some 125 species, which are divided into seven sections. In his treatment of the Gentianaceae in De Candolle's 'Prodromus' in 1845,[32] the number of species was increased to 153. In 1838 the

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[24] Necker, N. J., Elem. Bot. 2:11–14. 1790.
[25] Moench, loc. cit. 482. 1794.
[26] Schmidt, F. W., in Roemer's Archiv f. Bot. 1:3–23. 1796.
[27] Borckhausen, loc. cit. 1796.
[28] Froelich, J. A., Gent. Diss. 1796.
[29] Bunge, A., in Nouv. Mem. Soc. Imp. Nat. Moscou 1:197–256. 1829.
[30] Endlicher, S. L., Gen. Pl. 600. 1836–40.
[31] Grisebach, A. H. R., Gen. et Spec. Gent. 1839.
[32] DC. Prodr. 9:86–119. 1845.

North American species were treated separately by Grisebach in Hooker's 'Flora Boreali-Americana'.[33]

Huxley[34] in 1888 suggested a rearrangement of the family based on the position of the corolla glands. His MESOMELITAE includes the plants having glands at the base of the ovary, while his PERIMELITAE includes those with epipetalous glands. In 1860, Turczaninow[35] monographed *Gentiana* in his 'Monographische Beschreibung der Enzianen'.

In 1892, Murbeck[36] published a small study of the European ENDOTRICHAE which includes several new species with distribution maps of some entities. He failed to include keys to the species.

In 1894, Kusnezow[37] divided the Linnaean genus into two subgenera, EUGENTIANA and GENTIANELLA. His voluminous monograph covers his subgenus EUGENTIANA only. He made no attempt to revise subgenus GENTIANELLA beyond establishing characters to distinguish it. This monograph was later translated from the Russian into German and was published in parts from 1896 to 1904. Kusnezow[38] again maintained the subgenus GENTIANELLA in his treatment in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien' in 1895.

In 1896, Wettstein[39] monographed the European species of the section ENDOTRICHA, recognizing 27 species; and in 1900, he revised the North American species of the same section.[40] In 1896, Wettstein[41] segregated *Gentiana tenella* Rottb. from the section ENDOTRICHA, erecting a new section COMASTOMA.

In 1901, Th. Holm[42] presented a short revision of the Canadian species of the section CROSSOPETALUM of which he described three new species.

In 1917, Gilg[43] monographed the South American species of *Gentiana*, recognizing 182 species of subgenus GENTIANELLA and one species of the subgenus EUGENTIANA. In this work he created a series of divisions to which he assigned no rank.

Schustler[44] returned *Gentianella* to the rank of genus in 1923, incorrectly ascribing it to Borckhausen rather than to Moench.

In 1936, H. Smith[45] raised Hemsley's section MEGACODON of *Gentiana* to the rank of genus, and in 1937, Marquand[46] united the genus *Crawfurdia* to *Gentiana*, but relegated the section PTERYGOCALYX Maxim. of *Crawfurdia* to *Gentian-*

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[33] Hooker, W. J., Fl. Bor-Amer. 2:54. 1838.
[34] Huxley, T. H., in Jour. Linn. Soc. Bot. 24:101–124. 1888.
[35] Turczaninow, N., in Nat. Sci. Meetings, 34–35. 1860 (Not seen).
[36] Murbeck, Sv., in Acta Hort. Berg. 2^3:1–28. 1892.
[37] Kusnezow, loc. cit. 1896–1904 (German; Russian ed. 1894, not seen).
[38] Nat. Pflanzenfam. ed. 1, 4^2:85. 1895.
[39] Wettstein, R. V., in Denkschr. K. Akad. Wiss. Wien, math.-nat. Cl. 64:1–73. 1896.
[40] Oesterr. Bot. Zeitschr. 50:168–173, 189–195, 290–293. 1900.
[41] Oesterr. Bot. Zeitschr. 46:121–128. 1896.
[42] Ottawa Nat. 15:175–183. 1901.
[43] loc. cit. 1917.
[44] loc. cit. 1923.
[45] Smith, Harald, in Handel-Mazzetti, Symb. Sin. 7:950. 1936.
[46] Marquand, C. V. B., in Kew Bull. 134–180. 1937.

ella. In an earlier paper[47] he had merely excluded PTERYGOCALYX from *Gentiana*.

Yu-chuan Ma,[48] in 1951, raised the section CROSSOPETALUM to generic rank, naming the genus *Gentianopsis*, but discussed no synonymy. However, whether by design or accident, no earlier generic name would have been valid for this group.

General Morphology

The North American species of *Gentianella* are glabrous herbs. In habit the plants are branched or simple. Of the North American species, only *G. barbellata* is a true perennial; the others are either annual, biennial or perhaps winter annuals. Actual growth tests are needed to determine their life cycle.

The primary root is rather small in comparison with the size of the entire plant and is slightly thickened, forming a slender tap-root. As a rule there are few secondary roots. In *G. barbellata* there is a horizontal rhizome which apparently grows a few inches below the surface of the soil and sends vertical branches upward to the surface. At the surface level these branches thicken considerably and are enveloped in the basal rosette. These horizontal rhizomes seldom are collected and appear on only the occasional dried specimen. Probably collectors as a rule do not take the trouble to dig into the stony ground of alpine tundras!

The stems frequently become woody at the base and, in coarse plants such as *G. crinita*, they become hollow in the lower part. Variously developed stem-wings occur in many of the plants, or the stems may be prominently angled or striate. The wings, however, vary to such a degree that the character is of little diagnostic value. In some plants the wings are twisted spirally about the lower part of the stem. This feature greatly influences the symmetry of the phyllotaxy, so that the leaves, instead of being strictly decussate, show a distinct shift in their position at each successive node.

The leaves in *Gentianella* are glabrous as are those of the entire family. Basal leaves are spatulate to lingulate, and may be sessile or the blade may be attenuated rather sharply to a narrow, decurrent, connate, or clasping petiole. These leaves may wither early in the season. The shape of the median leaves is sufficiently diagnostic to be useful as a supporting character. In the fringed gentians the leaves usually have a single mid-vein; in the amarellas, arctophilas and comastomas the venation is palmate with three to five nearly parallel veinlets. The mid-vein is generally fairly prominent, while the laterals may or may not be distinct. Leaf margins are entire throughout the genus, occasionally minutely papillose or ciliate under magnification.

If a leaf be carefully pulled downwards and torn from the stem so that a fragment of the stem epidermis is removed with it, several minute processes or squamel-

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[47] Kew Bull. 66–68. 1931.
[48] loc. cit. 1951.

lae may be found attached to the base. These structures have been reported in other families of the Contortae, and may represent reduced stipules.[49]

The inflorescence is basically cymose, consisting of a simple cyme, an aggregate umbelliform cyme borne in a compact head, or may be reduced to a single terminal flower on a slender pedicel. Often flowers are borne singly or in pairs in the axils of the cauline leaves (dichasium). The upper leaves may frequently become bract-like and envelop the inflorescence, as in *G. aurea.*

The calyx is tubular in all species except *G. wislizeni* where the tube is split down one side to form a spathe, with the lobes reduced to minute teeth at the apical margin. Grossheim[50] described this condition for the European *G. ciliata* but I have never seen this type of calyx in any of the North American fringed gentians.

In subgenus EUBLEPHIS (the fringed gentians) there are four calyx lobes, probably representing an inner and an outer cycle. The lobes of this group are thinly membranaceous, usually hyaline-margined, the outer lobes frequently plicate and carinate at the tip. The sinuses of the calyx lobes have a small internal hyaline membrane which bears a row of minute blunt processes. The venation of the lobes of subgenus EUBLEPHIS is usually reticulate.

In subgenera GENTIANELLA and COMASTOMA there may be four calyx lobes or five forming a quincunx. The lobes vary in shape and length with respect to the tube and furnish useful characters. The calyx lobes of these two subgenera are somewhat fleshy. A mid-vein and two lateral veins occur and the laterals either unite below the sinus or at the base of the tube. Squamellae are usually found on the inner surface of the calyx tube near the base. These structures, however, are of little taxonomic value.

The corolla may be tubular, funnelform, or salverform when the lobes are fully expanded. In North American species its color varies from white to yellow, blue, and violet. South American species are often brilliant yellow or red. The lobes are oblong, obovate, ovate, to triangular, with acute, apiculate, mucronate, or obtuse tips. At the base of the lobes in many species there is a horizontal row of fimbriae (the crown) which may be free or may be united at the base to form a fringed scale. In section AMARELLA these fimbriae usually are continuous across the base of the lobe, sometimes irregularly scattered, with a vascular trace in each fimbria. In the COMASTOMAE, on the other hand, there are two separate fimbriate scales at the base of each corolla lobe and there are no vascular strands within the fimbriae. As in certain apocynaceous corollas, these scales may be of stipular origin.[51]

At the base of the corolla tube and alternate with the stamens are small glands or nectaries of various shapes. These never appear foveate, but are more frequently swollen. The glands are never accompanied by fimbriae.

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[49] Holm, R. W., in Ann. Mo. Bot. Gard. 37:484. 1950.
[50] Grossheim, A. A., in Fl. U. S. S. R. 18:591. 1952.
[51] Woodson, R. E. & Moore, J. A., in Bull. Torr. Bot. Club 65:135–165. 1938.

The stamens are equal in number to the corolla lobes and are alternate with them. Occasionally in *G. wislizeni* and *G. microcalyx* the anthers abort, with the staminodia elongate or reduced to small protuberances. The stamens are inserted near the center of the tube or below. The filaments usually are winged at the base, the wings curving inwards to form a canaliculate filament. The anthers are oblongoid or ovoid, and versatile, appearing introrse before dehiscence, then rotating and becoming extrorse following dehiscence. The three-pored pollen grains are essentially uniform in the genus.

The size and shape of the pistil are dependent upon the age of the flower. Prior to fertilization the style frequently is distinct; after fertilization it may gradually disappear with the maturation of the ovary and the formation of the capsule. The gynophore may also vary in length and distinctness with age. In some species the pistil is sessile or subsessile; in others the gynophore may be minute in young flowers, elongating considerably as the capsule matures. In some the gynophore always is elongate.

The two stigmas vary considerably in size and shape. They may be flabelliform and broad; or oblong, elliptic, or reniform and narrow. Their margins may be entire, sinuous or toothed—all features that vary within a population.

Seeds are of very great value to distinguish sections, but in most instances fail to separate species. Those of subgenus EUBLEPHIS are oblong and frequently angular, with reticulate or papillose surfaces. In two species, however, *G. simplex* and *G. ciliata* of Europe, they are reticulate and pronouncedly caudate. Those of subgenus GENTIANELLA series AMARELLAE and ARCTOPHILAE, as well as those of subgenus COMASTOMA, are round to slightly flattened. The color almost invariably is light brown.

Geographical Distribution

The genus *Gentianella* has an almost global distribution. In North America the two subgenera EUBLEPHIS and GENTIANELLA, have roughly a similar distribution but apparently different histories. Both groups have species that occur in Europe and Asia and connect with North America through either Greenland or Alaska. The variability and complexity found in the North American populations also occur in Asia and Europe. The South American species of the genus are placed chiefly in sections IMAICOLA and ANDICOLA.

In subgenus COMASTOMA only one widespread species, *G. tenella*, is represented in North America. This species occurs in Colorado south to Arizona and New Mexico, west to California, and in a few scattered stations across Alaska, Canada, and Greenland. The same species is common in Iceland, northern Europe and in the high mountains of southern Europe and Asia.

The fringed gentians (EUBLEPHIS) exhibit interesting distributional patterns. *G. simplex* and *G. barbellata* both occupy rather limited areas below the margin of maximum glaciation and probably have had quite an independent and

an older history than the *detonsa-crinita* complex. The seed of *G. simplex* of California bears a striking resemblance to that of *G. ciliata* of Europe. This seed similarity between these two species prompted Engelmann[52] to set up two groups or series of undesignated rank to indicate this relationship: a. Lepidospermae (*G. crinita, G. lanceolata, G. barbellata*), b. Pterospermae (*G. ciliata, G. simplex*). Seed similarity is the only major character that these two species have in common, so the classification of Engelmann may not represent true relationships. Recently Grossheim in the 'U.S.S.R. Flora' employed a similar division of the species (Series CILIATAE and BARBATAE) but based it on floral characters, apparently failing to note the distinct nature of the seed of *G. ciliata*.

If we hypothesize a Eurasian origin, there may have been several "invasions" of the *detonsa-crinita* complex into North America. The meagre, but no less valuable, chromosome data at hand indicate an $n = 13$ series represented by *G. crinita* and its ssp. *procera*, and an $n = 11$ series represented by *G. detonsa* (probably ssp. *detonsa*), hexaploid and tetraploid species respectively. The most stable portion of the complex is that occurring south of glaciation. Apparently the *crinita* group entered North America either from the north and reached the Appalachians, or arose independently there. The *detonsa* group perhaps entered through Alaska and migrated southwards as far as central Mexico with a branch into California (ssp. *holopetala*). Glaciation probably eradicated the group in the north except for a few isolated refugia. This may have been followed by a remigration back into the deglaciated area from Alaska-Yukon by means of the Yukon and Mackenzie River systems. The southern portion of the *detonsa* population was unable to move north perhaps through lack of suitable high altitude/high latitude habitat requirements. The *crinita* group, finding suitable low altitude/low latitude habitats, moved rapidly northwestward into the Great Lakes region and across the plains as far as the Rocky Mountains to close the population gap.

This broad conjectural outline may aid in understanding the subspecific treatment afforded this complex. The various populations are more or less imbricate in their distribution—or in the case of the *crinita* group, clinal—indicating a differentiating process accompanying the migration flow. Further discussion follows in the taxonomic treatment.

Study Material

Specimens or photographs from the following institutions have been available for the purpose of this study, either through loans or by visits to the herbaria. For

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[52] Engelmann, G., in Trans. Acad. Sci. St. Louis 2:216. 1868.

the sake of consistency, the abbreviations used are those listed by Lanjouw and Stafleu.[53]

A—Arnold Arboretum, Cambridge, Mass.
C—Universitets Botaniske Museum, Copenhagen, Denmark.
CAN—National Museum of Canada, Ottawa, Ont.
DAO—Botany and Plant Pathology Laboratory, Science Service, Canada Department of Agriculture, Ottawa, Ont.
F—Chicago Natural History Museum, Chicago, Ill.
GH—Harvard University Herbarium, Cambridge, Mass.
ID—Herbarium of the University of Idaho, Moscow, Ida. (This includes the Botany Herbarium and the Range Herbarium of the Department of Forestry).
JBM—Jardin Botanique de Montréal, Montréal, P. Q.
MEXU—Herbario Nacional del Instituto de Biologia de la Universidad Nacional de México, Mexico, D. F.
MO—Missouri Botanical Garden, St. Louis, Mo.
MIN—Herbarium, University of Minnesota, Minneapolis, Minn.
NY—New York Botanical Garden, New York, N. Y.
ND—Herbarium, University of Notre Dame (Greene-Nieuwland Herbarium), Notre Dame, Ind.
PH—Academy of Natural Sciences, Philadelphia, Pa.
S—Naturhistoriska Riksmuseum, Stockholm, Sweden.
SWC—Dominion Experimental Station, Swift Current, Sask.
UBC—University of British Columbia, Vancouver, B. C.
UC—Herbarium of the University of California, Berkeley, Calif.
US—United States National Herbarium, Washington, D. C.
WS—State College of Washington, Pullman, Wash.
RM—Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyo.

Citation of Specimens: For reasons of economy, citations have been considerably reduced. Specimens of species represented by little material have been cited in full. Those of common and widely distributed species have been reduced. One specimen from each county or, lacking counties, places or districts is cited. Individual collections have been selected for citation on the basis of breadth of distribution of duplicates or of historical importance.

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Taxonomic Treatment

Gentianella Moench, Meth. Pl. 482. 1794, emend. Schustler, in Vestnik Sjezdu Cesko Bot. v. Praze, 32–34. 1923. (T.: *Gentianella tetrandra* Moench based on *Gentiana campestris* L. Sp. Pl. ed. 1, 231. 1753 = *Gentianella campestris* (L.) Börner, Fl. deut. Volk, 543. 1912.)

[53] Lanjouw, J., and Stafleu, F. A., in Regnum Vegetabile 2. Index Herbariorum, p. 131. ed. 2, 1954.

Anthopogon Necker, Elem. Bot. 2:12. 1790, ut species; Raf. Fl. Tellur. 3:25. 1837, ut genus, non Nutt. Gen. N. Amer. Pl. 1:81. 1818.
Spiragyne Neck. loc. cit. 12. 1790, ut spec., nom. ambig.
Opsantha Delarb. Fl. d'Auvergne, ed. 2, 30. 1800.
Gentiana L. subg. *Gentianella* Kusnez. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, 4²:85. 1895.

Caulescent or acaulescent annual, biennial, winter annual, or perennial herbs, rarely shrubs (in South America), usually with tap-roots, rarely with slender rhizomes. Leaves opposite, membranaceous or fleshy, sessile or petiolate, usually palmately 3- to 5-veined, the veins prominent or inconspicuous. Inflorescence a terminal or axillary umbelliform dichasium, or an aggregate or simple cyme, frequently 1-flowered. Calyx 4- to 5-lobed, tubular, obconic, or 4-angulate, rarely spathiform, without an inner continuous membranaceous rim, carinate or ecarinate, glabrous or scabrous-papillose, frequently bearing a number of minute squamellae within and at the base of the tube. Corolla 4- or 5-lobed, marcescent, tubular, funnelform, campanulate, to rotate (in S. American species), the tube with or without faucal fimbriae; lobes with 5–9 parallel veins, sinistrally or quincuncially convolute in the bud, without interlobal plicae; interstaminal glands at the base of the tube (never at the base of the ovary) somewhat scutiform or rounded, swollen or appearing only as green patches on the surface of the tube, the glands never foveate. Stamens 4 or 5, included; filaments linear or variously taper-winged, rarely ciliate at the base; anthers 2-celled, oblong, rarely somewhat triangular, versatile, introrse in the bud but becoming extrorse following dehiscence. Ovary sessile or stipitate; carpels 2, 1-celled, the placentae parietal; stigmas 2, sessile or with a distinct style, oblong to flabelliform or reniform, lobed or entire, revolute or plane. Fruit a cylindrical or ovoid capsule, septicidally dehiscent from the apex. Seeds globose or slightly flattened, angular or caudate, reticulate, papillose or smooth, brown or light tan.

KEY TO THE SUBGENERA

a. Flowers 4-merous; calyx tubular, the lobes with thin hyaline margins, the sinuses with a small inner membrane extending across the base and bearing minute blunt processes; anthers distinctly longer than broad, attached in the upper third; ovules borne over the entire surface of the ovary; seeds oblong, oval, or angular, papillose or caudate.....Subgenus I. EUBLEPHIS

aa. Flowers 4- or 5-merous; calyx tubular, rarely spathiform, the lobes with a green margin, the sinuses without an inner membrane; anthers slightly longer than broad, filaments attached at about the middle; ovules borne in two rows along the margin of each suture, rarely with a third row along the carpel wall between the sutures; seeds globose or slightly flattened, smooth, ecaudate.

b. Pedicels conspicuously shorter than the subtending internode; corolla orifice naked, or bearing scattered vascular minutely papillose fimbriae, or the fimbriae united to form a single scale extending across the base of each corolla lobe.............Subgenus II. GENTIANELLA

bb. Pedicels conspicuously longer than the subtending internode; corolla orifice bearing two fimbriate scales at the base of each corolla lobe, the fimbriae shortly digitate, evascular, smooth...Subgenus III. COMASTOMA

Subgenus I. EUBLEPHIS (Raf.) J. M. Gillett, comb. nov.

Gentiana L. subgenus *Eublephis* Raf. Med. Fl. 1:208. 1828. (T.: *G. crinita* Froel.)
Gentianella Borckh. in Roem. Archiv f. Bot. 1:29. 1796, non Moench. (T.: *G. ciliata* (L.) Borckh.)
Gentiana L. **** *Crossopetalae* Froel. Gent. Diss. 109. 1796, sine ordine.
Denckea Raf. in Med. Repos. II, 5:352. 1808, nom. nud.
Crossopetalum Roth, Enum. Pl. Phaen. Germ. 1:516. 1827. (T.: *C. gentianoides* Roth = *Gentiana ciliata* L.)
Gentiana L. *Urananthe* Gaud. Fl. Helv. 2:270, 1828, sine ordine.
Gentiana L. sect. *Crossopetalum* Froel. ex Griseb. in Hook. Fl. Bor. Amer. 2:64. 1838.
Gentianopsis Ma, in Acta Phytotax. 1:7. 1951. (T.: *G. barbata* (Froel.) Ma)

Flowers usually large and showy, 4-merous, long-pedicellate. Calyx usually 4-angulate, the lobes with thin hyaline margins, the two inner triangular to ovate, the two outer linear to lanceolate, acute, and usually conduplicate and the margins united at the tips, each sinus with a thin inner membrane bearing few to many blunt processes. Corolla tube without faucal fimbriae, the lobes with reticulate venation connecting the main veins. Stamens inserted near the middle of the tube. Ovary with the parietal placenta extending over most of the inner surface. Seeds ellipsoid to angular, minutely or strongly papillose, or caudate, light brown.

Tetraploids or hexaploids on base numbers of 11 and 13.

Type species: *Gentianella crinita* (Froel.) G. Don.

KEY TO THE SPECIES

a. Plants in general branched, occasionally simple (but usually occurring among populations of branched plants), with a definite rosette of basal leaves or a tendency to form a rosette by shortening of the lower internodes; flowers solitary or in axillary or terminal cymes; seeds ecaudate, the surface papillose.
  b. Terminal flowers borne on slender pedicels extending beyond the upper pair of leaves; corolla tube glabrous below the insertion of the stamens; annuals or biennials with tap-roots.
    c. Base of the calyx and the calyx keels smooth or wrinkled, the keels glossy purple; upper leaves usually obtuse.......1. *G. detonsa*
    cc. Base of the calyx near the junction with the pedicel and usually at least one pair of calyx keels covered by whitish or hyaline papillae (under magnification) occasionally present also on the margins of the lobes, the keels green or purple; upper leaves acute.......2. *G. crinita*
  bb. Flowers sessile or shortly pedicellate, the uppermost pair of bract-like leaves immediately below the flower and subtending it; corolla tube bearing rows of long cilia below the insertion of the stamens; perennials from slender rhizomes.......3. *G. barbellata*
aa. Plants simple, never branched, without a basal rosette of leaves; the single flower borne terminally on an elongate naked pedicel; seeds caudate, the surface reticulate.......4. *G. simplex*

While *G. simplex* and *G. barbellata* are both morphologically and geographically very sharp, clear-cut populations, the *G. detonsa-crinita* complex is much less convincing. The complex may be considered either as one large species or divided into two rather weak species. The presence or absence of papillae on the calyx keels is a constant character differentiating these species. The obtuse or rounded medium leaf tips of the *detonsa* group versus the acute tips of the *crinita* group is a strong supporting character. Other characters either vary considerably or are influenced both by plant age or by the presence of the small form of the plant found so commonly among the larger members of a population.

I have chosen to recognize *G. detonsa* and *G. crinita* as two separate species for the following reasons: 1. *Gentianella crinita* ssp. *crinita* has an Appalachian distribution probably indicating an older history than that of *G. detonsa.* 2. The disjunction between the non-papillose northern *G. detonsa* ssp. *raupii* and the central ssp. *elegans* can be more readily explained. 3. The presence of the narrow-leaved papillose-keeled ssp. *macounii* between these two disjunct populations can best be explained by migration. 4. Present-day scant cytological evidence in the group indicates the presence of at least two chromosome series, the *detonsa* series with a base number of 11 and the *crinita* series with a base number of 13. 5. The occasional presence of sterile and depauperate forms in Manitoba may be due to occasional crosses between members of these two chromosome series.

1. Gentianella detonsa (Rottb.) G. Don, Gen. Syst. 4:179. 1838.

Gentiana detonsa Rottb. Kiob. Selsk. Skr. (Acta Hafn.) 10:435. 1770. (T.: *Collector unknown,* herb. Rottböll, C!)

Annuals or biennials, 0.5–9.0 dm. tall, branched from the base or above, or simple, the basal branches curved or straight, shorter than (or nearly equal to) the main stem. Basal leaves elliptic, obovate-elliptic to spatulate, the apex rounded, obtuse, or acute, attenuate below to about the width of the stem, 0.5–3.5 (–6.0) cm. long, 0.1–1.5 cm. wide, forming a dense rosette, or frequently reduced to one pair; median leaves linear or linear-lanceolate to elliptic or spatulate, usually rounded, the base attenuate to about the width of the stem or slightly broader, frequently subamplexicaul or clasping, 1.5–6.5 cm. long, 0.1–0.7 cm. wide. Flowers solitary and terminal, long-pedicellate, the terminal pedicels 1–30 cm. long, those of the basal or lateral branches when present shorter, occasionally equal. Calyx narrowly to broadly funnelform, the tube 9–14 mm. long, 5–7 mm. wide below the lobes, the inner lobes ovate-triangular, acute, about 10 mm. long, the outer lobes longer, lanceolate and conduplicate, frequently carinate at the tip, acute, up to 14 mm. long or equal to the inner lobes; keels 1 mm. or less wide, scarcely prominent, smooth and reticulate, generally purple-tinged; sinuses acute, covered on the inside by a small straight to sulcate membrane extending to the center of the outer lobes and bearing few to many blunt processes up to 0.5 mm. long. Corolla pale to dark blue, narrowly funnelform, 2–4 (–5) cm. long, 4–10 (–15) mm. wide at the orifice, the lobes oblong or somewhat expanded above, 9–15 mm. long, 5–7 (–15) mm. wide, the tips erose to denticulate, the margins with few to several cilia 0.5–1.5 mm. long in the lower half. Stamens included, the filaments inserted near the middle of the corolla tube, the marginal wings 1.5 mm. wide at the base, tapering gradually above; anthers 2.5 mm. long, 1.0 mm. wide, attached above the middle; interstaminal glands oblong, crescent shaped to rounded, swollen below and tapering to the tube above. Pistil short-stipitate, the gynophore 2–4 mm. long, obscurely attenuate; ovary fusiform, about 12 mm. long, 2.0 mm. wide; stigmas sessile or short-stipitate, flabelliform, reniform, or oblong, 1.75 mm. wide. Capsule as long as the corolla tube or slightly longer, dehiscing in the upper

third, the tips of the valves recurving. Seeds ovoid to oblong, slightly flattened, the surface reticulate and with slender or rounded, inflated or somewhat collapsed hyaline papillae irregularly dispersed or concentrated at the angles and ends.

Circumboreal, extending from North America to Europe through Greenland and Iceland, and to Asia through Siberia; in North America from both the east and the west coasts of Greenland as far north as Disko and Cape Oswald, on the mainland westward to Coppermine and Kotzebue, southward on the east to Quebec and Newfoundland and on the west through Alaska and the Yukon through the Rocky Mountains and the Sierra Nevada to the Sierra Madre of Mexico; resolving into several subspecies and numerous minor local variants.

In a variety of habitats: tidal estuaries, river banks, mountain meadows, saline meadows, about hot springs and sloughs, in open or sparsely wooded plains, but in general preferring lime soils or shallow soil over limestone; flowering and fruiting times various depending upon latitude but generally from late June until November; at altitudes from sea-level to 2500 meters.

KEY TO THE SUBSPECIES

a. Margins of the corolla lobes ciliate at least in the lower half, the tips erose to dentate; pedicels 2–15 cm. long; gynophore short, never as long as the capsule; interstaminal glands not swollen.

b. Seeds oblong with smoothly rounded ends, the elongate inflated or collapsed and scale-like whitened papillae restricted to the ends, occasionally absent; calyx tube attenuate to the pedicel, not abruptly constricted; corolla slender, 4–9 mm. wide at the frequently constricted or scarcely expanded orifice, the tube narrowly obconic. Arctic coast and west of the Mackenzie Mountains.

c. Plants 0.5–1.8 dm. tall, simple or the branches arising from the base; basal rosette poorly developed or reduced to a single pair of leaves. Circumboreal above the northern limit of trees, Kotzebue to Coppermine and the coast of Greenland...1a. *G. detonsa* ssp. *detonsa*

cc. Plants 2–6 dm. tall, simple or the branches arising from the axils of cauline leaves, rarely from the base; basal rosette well developed, the leaves dense, rarely reduced particularly in smaller specimens. Yukon and Alaska, chiefly along the Yukon River and its tributaries..1b. *G. detonsa* ssp. *yukonensis*

bb. Seeds irregularly angled, the rounded, inflated, light-brown papillae distributed over most of the surface; calyx tube abruptly constricted to the pedicel; corolla 8–15 mm. wide at the distinctly expanded orifice, the tube rather broadly obconic or poculiform.

d. Flowers 1–4 cm. long, rarely longer, 0.5–1.2 cm. wide at the orifice, the keels of the calyx not prominent; cauline leaves elliptic to spatulate.

e. Plants usually short, 0.5–1.2 (–2.0) dm. high, profusely branched from the densely spatulate-leaved base, the green or purpled branches curved-ascending; corolla lobes somewhat short and truncate, about ⅓ to ½ the length of the tube. East coast of James Bay, Anticosti and Newfoundland......................1c. *G. detonsa* ssp. *nesophila*

ee. Plants generally tall, 3–6 dm. high, branched above, occasionally simple in small plants, the branches and stem frequently sinuous and strongly purpled; corolla lobes elongate and rounded, about equal in length to the corolla tube. A highly variable complex extending from the Mackenzie Valley east to Hudson Bay...1d. *G. detonsa* ssp. *raupii*

dd. Flowers up to 7 cm. long and 1.6 cm. wide at the orifice, the keels of the calyx prominent, particularly at the base of the tube; cauline leaves lanceolate to elliptic.

f. Terminal pedicels of mature plants 4–12 (–16) cm. long; flowers 3–5 (–7) cm. long; plants generally branched from the base. Central Rocky Mountain states...1e. *G. detonsa* ssp. *elegans*

ff. Terminal pedicels 9–30 cm. long; flowers 4.5–8.0 cm. long; plants generally branched above the base. Southern Arizona; in the Sierra Madres south to Zacatecas...1f. *G. detonsa* ssp. *superba*

aa. Margins of the corolla lobes entire, devoid of any fimbriae or teeth, the tips entire to erose; pedicels 2–3.5 cm. long.

g. Plants 4–9 dm. tall, branched in the upper part, rarely simple; gynophore short, about 5 mm. long; calyx keels rarely papillose; interstaminal glands frequently free at the base and pendent. Southern Sinaloa and Zacatecas to Michoacán...1g. *G. detonsa* ssp. *lanceolata*

gg. Plants 0.3–4.5 dm. tall, branched from the base or simple; gynophore frequently almost as long as the capsule, 8–11 mm. long; calyx keels always smooth; interstaminal glands swollen below and fused to the corolla tube. California to western Nevada and Idaho. ....1h. *G. detonsa* ssp. *holopetala*

1a. Gentianella detonsa (Rottb.) G. Don, ssp. detonsa

Gentiana ciliata Gunn. Fl. Norv. 2:88. *t. 2. f. 3–5.* 1772, ex ic.
Gentiana serrata Gunn. loc. cit. 2:101. 1772, ex char.
Gentiana ciliata Pall. Fl. Ross. 1^2:101. *t. 92. f. 2a.* 1788, ex ic.
Gentianella serrata (Gunn.) Borckh. in Roem. Archiv f. Bot. 1:29. 1796.
Gentiana barbata Froel. Gent. Diss. 114. 1796, ex char.
Gentiana serrata Gunn. β *detonsa* (Rottb.) Wahl. Fl. Lapp. 71. 1812.
Gentiana barbata Froel. β *simplex* Bunge, in Nouv. Mem. Soc. Nat. Mosc. 1:224. *t. 9. f. 1.* 1829, ex ic.
Gentiana brachypetala Bunge, loc. cit. 225. *t. 9. f. 3.* 1829, ex ic.
Gentiana barbata Froel. γ *Richardsoniana* Macnab, in Edinb. New Phil. Jour. 19:62. 1835. (T.: *Richardson s.n.*, MO, photo!)
Anthopogon detonsa (Rottb.) Raf. Fl. Tellur. 3:25. 1837.
Anthopogon barbata (Froel.) Raf. loc. cit. 25. 1837.
Gentiana detonsa Fries β *barbata* (Froel.) Griseb. in Hook. Fl. Bor.-Amer. 2:64. 1838.
Gentiana detonsa Fries γ *simplex* (Bunge) Griseb. loc. cit. 1838.
Gentiana detonsa Rottb. var. *groenlandicum* Vict. in Contr. Lab. Bot. Univ. Montréal 20: 18. 1932. (T.: *Porsild & Porsild s. n.*!)
Gentiana richardsonii Porsild, in Nat. Mus. Can. Bull. No. 121:274–275. 1951. (T.: *Porsild 2653*!)
Gentianopsis barbata (Froel.) Ma, in Acta Phytotax. 1:8. 1951.
(Synonyms referring to other Eurasian types are not included).

Subspecies *detonsa* has a circumboreal distribution but appears to occupy rather localized areas within its range. It occurs in Finland, Norway and Iceland, on both east and west coasts of Greenland, in America and Asia. Between Greenland and Coppermine, District of Mackenzie, the disjunction in distribution is constantly being reduced by additional collections. Westward, subspecies *detonsa* occurs at Atkinson Point at the mouth of the Mackenzie, at Kotzebue Sound, and after a further gap, in Mongolia and Siberia, being notably absent from Kamchatka.

Found in moist meadows, along sandy sea beaches; flowering from mid-July to early August; fruiting in August.

I have included *G. barbata* within the synonymy of this subspecies in order to emphasize that the name *barbata* should not be applied to our North American material. *G. barbata,* if considered to be distinct at a later date, applies to the taller Eurasian material and appears to be transitional to ssp. *detonsa*. In this view I follow in part Grisebach, because I have had little European material at my disposal. However, our North American material in my opinion is not identical with the taller European material nor with the various species from Asia illustrated by Yu-chuan Ma in his recent revision.

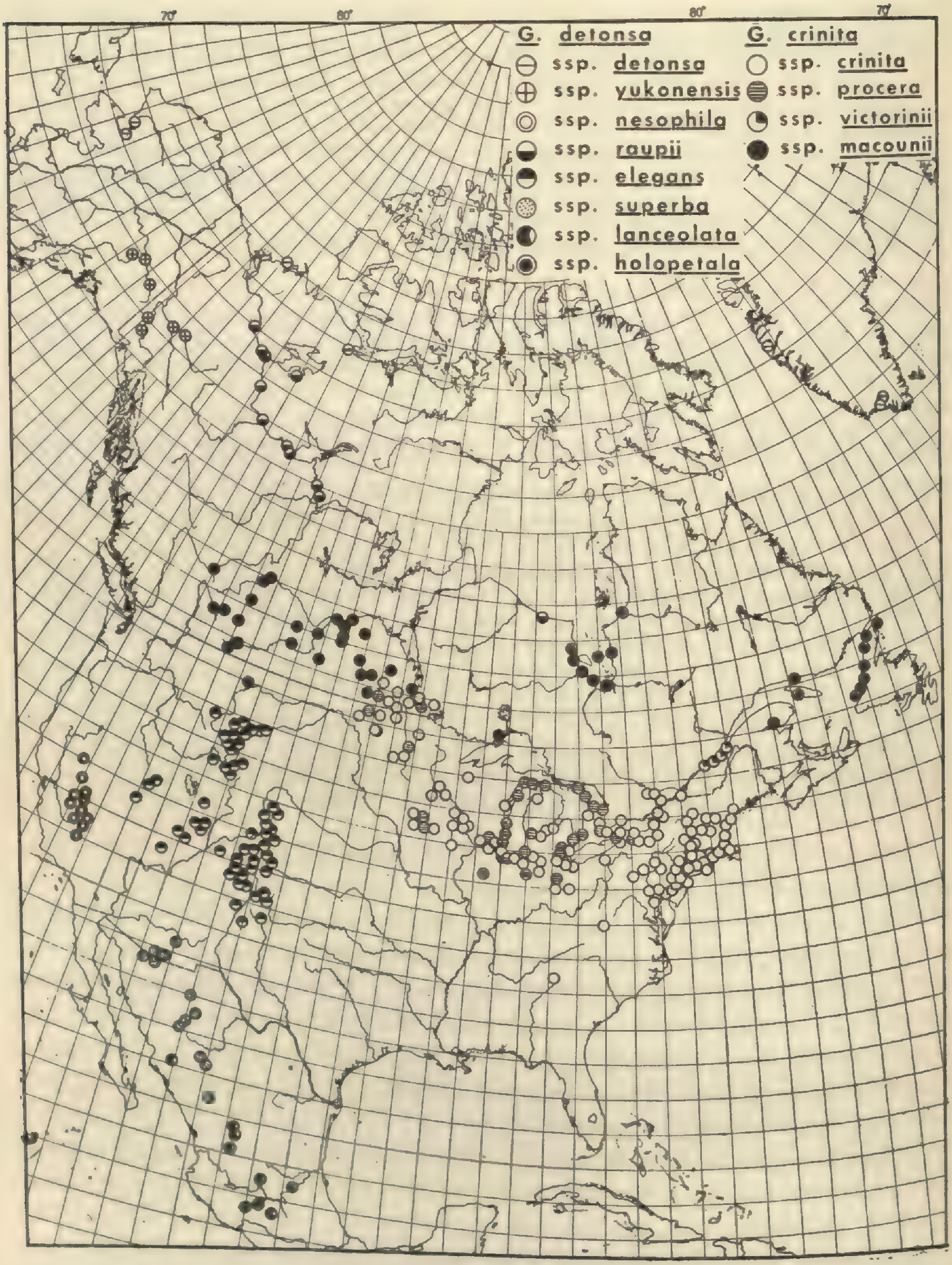

Fig. 1A. Distribution of the subspecies of *Gentianella detonsa* and of *G. crinita.*

NOTE: Through an error in drawing, the symbols for *G. detonsa* ssp. *nesophila* and ssp. *holopetala* have been interchanged.

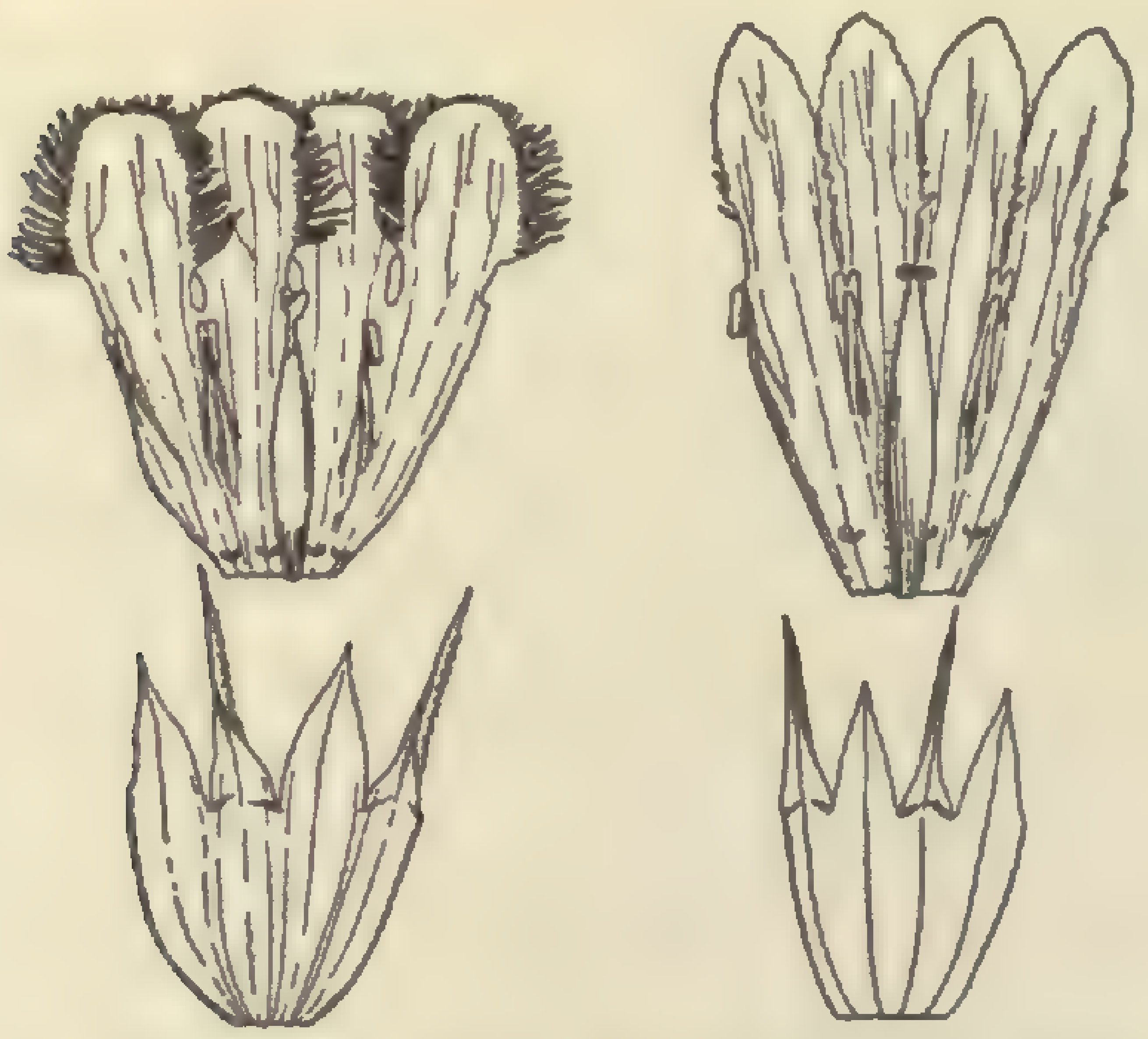

Fig. 1B. Calyx and corolla of *Gentianella detonsa* ssp. *detonsa* (right, approx. nat. size) and of *G. crinita* ssp. *crinita* (left, × ½).

UNITED STATES:

ALASKA: Keewalik Spit, *Miller 25c* (US); Kotzebue, *Anderson 4683b* (S), *4766* (S), *Lepage 25406* (DAO), *Scamman 4063* (GH), *4663* (CAN).

GREENLAND: Igdungujak, *Hott s. n.* (C); Ekaluit i Igalikofjord, *Lindemann s. n.* (C); Itivdleq-Fjord, Qingua, *Porsild s. n.* (C, CAN, MO, US); Igaliko (Gardar), *Porsild & Porsild s. n.* (C, CAN, GH, JBM, US), *Rosenvinge s. n.* (C, CAN), *Vahl s. n.* (C); Julianehaab, *Rosenvinge s. n.* (C), *Vahl s. n.* (C), *Porsild 8085* (CAN).

CANADA:

MACKENZIE: Coppermine, *Findlay 241* (DAO); Atkinson Point, 70° N, 131° 20′ W, *Porsild & Porsild 2653* (CAN).

1b. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. **yukonensis** J. M. Gillett, subspec. nov.

Herbae annuae. Caules erecti, 2–6 dm. alti, simplices sive ramosi, ramis ex axillis foliorum caulinarium interdum radicalium emergentibus. Folia radicalia pluralia in rosulam congesta elliptica vel spathulata apice obtusa, 6–25 mm. longa, 5–10 mm. lata; folia media linearia vel lineari-lanceolata, 20–60 mm. longa, 1–6 mm. lata. Flores et semina subspeciei typica similes.

Although variation in subspecies *detonsa* is rather high and the distribution is circumboreal, there appears to be considerable justification in erecting this new subspecies based chiefly on size difference and mode of branching. A prominent morphological feature is the dense rosette of basal leaves. Floral and fruit morphology is essentially similar to the typical subspecies but the flowers are slightly larger. Habitat data appearing only on modern collections show that it is found in sandy and gravelly places. *Cody & Webster 5587* has been selected as the type because the material is of good quality and because several duplicate sheets are available for distribution.

The range of subspecies *detonsa* corresponds rather closely to that region north of the Nordenskiold line which in turn roughly corresponds to the northern limit of trees in North America. Subspecies *yukonensis* occurs south of this line and apparently is restricted to the valley of the Yukon River and its tributaries.

United States:

alaska: Tanacross, *Anderson s. n.* (S); Mackintosh, *Anderson & Brown 10065* (S); between Summit and McCarty, *Porsild & Porsild 440* (CAN, GH, US); near Delta Junction, *Cody & Webster 5599, 5717* (DAO); Big Delta, *Cody & Webster 6154* (DAO), *Lepage 25325* (CAN); Buffalo Center nr. Big Delta, *Anderson 8939* (CAN); Fort Yukon, *Houle s. n.* (CAN); scattered along sandy roadside, Mile 265, Richardson Highway, 4 miles south of Delta Junction, 60° 00′ N, 145° 45′ W, June 28, 1951, *W. J. Cody & T. J. M. Webster 5587* (DAO, holotype).

Canada:

yukon: Pelly River, Mayo District, *Bostock 226* (CAN); Ranch Valley, *Gorman 1081* (CAN, NY, US); Snag Airport, *Noel 38* (UBC), *14184* (CAN); Lake Kluane to Don Jek River, *Müller s. n.* (PH); above Fort Selkirk, *Tarleton 115a* (US), *115b* (NY); Cormacks, Yukon River, *Eastwood 567* (CAN).

1c. Gentianella detonsa (Rottb.) G. Don, ssp. **nesophila** (Th. Holm) J. M. Gillett, comb. & stat. nov.

Gentiana nesophila Th. Holm, in Ottawa Nat. 15:11. 1901. (T.: *Macoun s. n.*!)

Northwestern Newfoundland, the Mingan Islands and Anticosti, and on the east coast of James Bay, on sandy or gravelly calcareous soil, at elevations from sea level to about 20 meters; flowering from late July until early September, fruiting from August until October.

Canada:

keewatin: Boat Opening, Manitounuk Island, *Dutilly & Lepage 12944* (DAO), *13021* (CAN); South Twin Islands, *Johansen 273* (CAN).

newfoundland: Cape St. George, *Mackenzie & Griscom 11121* (GH); Cape Norman, *Wiegand & Long 28927* (GH); Cook Point, *Fernald, Gilbert & Hotchkiss 28928* (GH); Brig Bay, *Fernald, Long & Dunbar 26969* (GH); Cow Head north of St. Paul's Bay, *Fernald & Wiegand 3898* (GH); Port au Port ("The Gravels"), *Fernald & Wiegand 3900* (CAN, GH, US); Old Ferolle, *Huntsman s. n.* (GH); Flower's Cove, *Fernald, Long & Dunbar 26970* (GH); Straits of Belle Isle, Mistaken Cove, *Fernald, Long & Dunbar 26966* (GH); Raleigh, *Jeffers 141* (GH); Old Port au Choix, St. Barbe, *Tuomikoski 355* (CAN); St. John Bay, Bard Harbour, *Fernald & Long 28925* (GH); Savage's Island, *Fernald, Long & Fogg 1959* (GH); St. Barbe, *Fernald, Long & Dunbar 26967* (GH, US); Bonne Bay, *Fernald, Long & Fogg 1961* (GH); Ingornachoix Bay, *Fernald & Wiegand 3899* (GH).

ontario: Attawapiskat, *Dutilly & Lepage 15797* (CAN).

quebec: Anticosti Island, nr. Salt Lake, *Macoun s. n.* (CAN); mouth of Jupiter River, *Wyatt, Shaler & Verrill, s. n.* (GH), *Rousseau 52411* (JBM), *Victorin & Rolland 25137* (CAN), *25197* (GH, US); Sand-top, *Victorin, Rolland & Louis-Marie 21069* (CAN, GH, MO, US); Mingan Islands, *Victorin & Rolland 21068* (GH, MO); Ile Sainte-Genevieve, *Victorin & Rolland 21066* (GH); Pointe de Betchouane, *Victorin & Rolland 21067* (CAN, GH, MO, US); James Bay, Baie aux Oies, *Lepage 12927* (CAN, DAO, JBM); Fort George, *Low s. n.* (CAN); Vieux Comptoir, *Dutilly & Lepage 13389* (CAN), *32057* (JBM); Kegashka Bay, *Lewis s. n.* (CAN).

The population of ssp. *nesophila* is relatively distinct but there are occasionally specimens from Newfoundland that resemble the typical subspecies rather closely. James Bay material frequently approaches ssp. *raupii* (for example, *Lepage 12877*, CAN).

1d. Gentianella detonsa (Rottb.) G. Don, ssp. **raupii** (Porsild) J. M. Gillett, comb. & stat. nov.

Gentiana raupii Porsild, in Sargentia 4:60. 1943. (T.: *Porsild 6571*!)

Sandy river shores, clay banks and salt plains along the Mackenzie River basin at low elevations, with scattered stations along Hudson Bay; flowering from late June to early August; fruiting in August.

Canada:

ontario: Raft River, James Bay [?], *Spreadborough s. n.* (CAN); Weenusk, *Dutilly & Lepage 16925* (DAO); Swan River, *Lepage 31666* (DAO).

mackenzie district: Wood Buffalo Park, Moose Lake, *Raup 3026* (CAN); Fort Norman, *Kindle s. n.* (CAN); Norman Wells, *Wynne-Edwards 8564* (CAN); Ramparts, Mackenzie River, *Porsild & Porsild 3403* (CAN); Great Bear Lake, McVicar Arm, *Wynne-Edwards 8617* (CAN); Heart Lake, *Raup 3028* (CAN); Great Slave Lake, *Howe 1026* (CAN); Sulphur Bay, *Howe s. n.* (CAN); Brabant Island, *Lewis 1074* (DAO); Mackenzie River betw. Wrigley and Blackwater River, *Porsild 6571* (CAN, photo DAO), *Crickmay s. n.* (CAN); Hay Camp District, Slave River, *Raup 3027* (CAN); Fort Wrigley, *Lindsey 296* (CAN); Mackenzie delta, east branch, *McEwan 47* (CAN); Fort Simpson, *Nowosad 4* (DAO); Fort Smith, *Cody & Loan 3783, 4169* (DAO); Mackenzie River, *Hutton s. n.* (DAO), *Jones s. n.* (CAN).

This subspecies must for the present remain a *pot-pourri* for that heterogenous assemblage of material occupying the Mackenzie Valley and extending to Hudson Bay in the east. The southern boundary of the subspecies is ill defined because the northern prairie provinces and southern districts of Mackenzie and Keewatin are still poorly collected. In the Hudson Bay and James Bay regions some specimens approach ssp. *nesophila.*

As the *detonsa* complex invaded the regions formerly occupied by the ice the movement was apparently accompanied by a segregation of numerous minor local variants. Variation was also produced by local environmental factors and resulted in a bewildering array of forms any of which may crop up with little regard for geographical continuity.

1e. Gentianella detonsa (Rottb.) G. Don, ssp. **elegans** (A. Nels.) J. M. Gillett, comb. & stat. nov.

Gentiana thermalis O. Ktze. Rev. Gen. 2:427. 1891, ex char. (T.: *Kuntze s. n.*)
Gentiana elegans A. Nels. in Bull. Torr. Bot. Club 25:276. 1898. (T.: *A. Nelson 1539*!)
Gentiana elegans A. Nels. var. *unicaulis* A. Nels. loc. cit. 277. 1898. (T.: *Nelson 4173*!)
Gentiana elegans A. Nels. var. *brevicalycina* Wettst. ex Th. Holm, in Ottawa Nat. 15:182. 1901, ex char.
Anthopogon elegans (A. Nels.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.
Anthopogon thermalis (O. Ktze.) Rydb. in Fl. Rocky Mts. 659. 1917.

I have followed the general practice of employing the oldest specific epithet for my subspecies in accordance with Recommendation 71A, Part 2 of the Rules (1950 ed. Stockholm). In some cases, however, where doubt exists concerning the location or identity of the type of the earliest specific name, I have chosen the next epithet for which a widely distributed or well-preserved type exists. The epithet *elegans* has been selected here, rather than *thermalis*, because it is more

widely known and because Nelson's specimen is of fine quality and is distributed among at least three herbaria and probably more. Kuntze's specimen has not been found. Rydberg, in making the combination *Anthopogon thermalis,* remarked "*G. thermalis* Kuntze, based on depauperate specimens."

Common throughout the Rockies from southern Montana to Wyoming, Utah and Idaho, west to eastern Nevada, south to New Mexico; in mountain meadows and along streams and roadsides; frequent about hot springs; flowering throughout July and August; fruiting in late August and September.

UNITED STATES:

COLORADO: Archuleta Co.: Chromo, *Wooton 2910* (US). Boulder Co.: Ward, *Clokey 2741* (US). Chaffee Co.: Buena Vista, *Maguire & Piranian 12856* (GH, MO). Clear Creek Co.: Wet Mountain Valley, *Horner s. n.* (GH). Conejos Co.: Cumbres Pass, *Babcock 9666* (GH). Custer Co.: Sangre de Cristo Range, *Ewan 15390* (GH). Eagle Co.: Leadville Forest, *Eggleston 11780* (US). Garfield Co.: Trapper's Lake, *Hermann 5472* (GH, MO, US). Grand Co.: Middle Park, Grand Lake, *Engelmann s. n.* (MO); Shapler Park, *Clokey & Clokey 4238* (MO, US, WS). Grant Co.: Rabbit Ears Pass, *Baker 7* (US). Gunnison Co.: Kebler Pass, *Baker 785* (GH, MO). Jackson Co.: Mt. Richtophen, *Baker 6* (US). Lake Co.: Twin Lakes, *Wolf 789* (US). La Plata Co.: Rockwood, *Evermann s. n.* (US). Larimer Co.: Cameron Pass, *Baker s. n.* (MO); Estes Park, *Allen 113* (MO). Mineral Co.: Pagosa Peak, *Baker 522* (GH, MO, US). Park Co.: South Park, Jefferson, *Letterman s. n.* (MO). Routt Co.: Columbine, *Tweedy 4098* (US). San Juan Co.: Silverton, *Popenoe s. n.* (MO, PH). San Miguel Co.: Trout Lake, *Payson & Payson 4116* (GH, MO). Summit Co.: Breckenridge, *Brandegee s. n.* (MO, NY).

IDAHO: Bannock Co.: Blackfoot River, *Eggleston 10002* (US). Bingham Co.: 10 mi. nw. Gray's Lake, *Gillett, Senn & Frankton 6039* (DAO). Fremont Co.: Henry's Fork, Snake River, *Coulter s. n.* (US); Henry's Lake, *Rydberg & Bessey 4695* (GH, US).

MONTANA: Carbon Co.: Rock Creek, *Elliott 76* (DAO, GH). Gallatin Co.: Gallatin basin, *Blankinship 351* (MO, US); 8 mi. w. Eldridge, *Hitchcock & Muhlick 15132* (MO, WS). Madison Co.: Beaver Creek, *Hitchcock & Muhlick 15120* (MO, WS); Madison Forest, *Schwan s. n.* (ID). Park Co.: 2 mi. s.e. Cooke City, *Hitchcock & Muhlick 13617* (GH, MO, US, WS). Stillwater Co.: Absaroka Nat. Forest, *Hitchcock & Muhlick 13406* (MO, WS).

NEVADA: Elko Co.: Ruby Valley, *Heller 9531* (GH, MO, NY, PH, US). Eureka Co.: *Brandegee s. n.* (MO).

NEW MEXICO: Colfax Co.: Ute Park, *Standley 14469* (GH, US). Mora Co.: Santa Fe Forest, *Eggleston 19031* (NY, US). Santa Fe Co.: Santa Fe, *Alcott s. n.* (MO). Taos Co.: La Junta Canyon, *Marcelline 2150* (F, WS). Sandoval Co.: Jemez Mts., *Goodwin s. n.* (GH).

UTAH: Custer Co.: Wet Mountain Valley, *Bacigalupi 983* (GH). Grand Co.: La Sal Mts., *Payson & Payson 4075* (GH, MO). Iron Co.: Cedar Canyon, 15 mi. e. Cedar City, *Hitchcock, Rethke, & Van Raadshooven 4635* (US, WS). Emery Co.: 10 mi. w. Castle Dale, *Maguire & Richards 15931* (GH, MO). Sanpete Co.: e. of Mount Pleasant, *Tidestrom 1887* (US). Sevier Co.: Fish Lake, *Jones 5777* (US). Summit Co.: La Motte Peak, *Jones s. n.* (MO, US), *Payson & Payson 5108* (GH, MO, US); Wasatch Mountains, *Clos 130* (US). Wayne Co.: Rabbit Valley, *Ward 607* (MO, US).

WYOMING: Albany Co.: Medicine Bow Mts., *Nelson 1539* (GH, MO, RM); Lincoln Gulch, *Nelson 8007* (GH, MO, US); Centennial, *Nelson 8709* (GH, MO, US); Telephone Mines, *Nelson 7888* (GH, MO, US). Carbon Co.: Medicine Bow Mts., Silver Lake, *Ownbey 325a* (WS). Lincoln Co.: Grey's River, *Porter 5175* (DAO). Park Co.: Shoshone Nat. Forest, Beartooth Lake, *Williams & Williams 3728* (GH, MO). Sublette Co.: Wind River Mts., *Forwood s. n.* (US); Surveyor Park, Fremont Lake, *Payson & Payson 2827* (GH, MO). Teton Co.: Jackson's Lake, *Merrill & Wilcox 1082* (GH, US). Yellowstone National Park: Lower Geyser Basin, *Thompson 14159* (GH, MO, US, WS); Upper Geyser Basin, *Mearns 473* (US); Yellowstone Lake, *Nelson & Nelson 6764* (GH, MO, US).

1f. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. **superba** (Greene) J. M. Gillett, comb. & stat. nov.

Gentiana macrocalix Lex. in La Llave & Lex. Nov. Veg. Descr. 1:19. 1824, ex char.
Gentianella macrantha D. Don, ex G. Don, Gen. Syst. 4:179. 1838, ex char.
Gentiana ciliata Moc. & Sessé, ex G. Don. loc. cit. 119. 1838, nom nud. in syn.
Gentiana macrantha (D. Don, ex G. Don) Griseb. in DC. Prod. 9:102. 1845.
Gentiana serrata Gunn. var. *grandis* A. Gray, Syn. Fl. N. Amer. 2:116. 1886. (T.: *Wright 1658*!)
Gentiana superba Greene, Pittonia 1:155. 1888. (T.: *Forrer 44*!)
Gentiana grandis (A. Gray) Th. Holm, in Ottawa Nat. 15:110. 1901.

As explained under ssp. *elegans*, I have tried to select as subspecific names the earliest ones available, or those most widely known (although not obliged to do so). I believe this course more reasonable than to propose entirely new names. In ssp. *superba* the earliest name was not selected because of difficulty in the identity or location of types.

The type of *Gentiana macrocalix* Lex. is given as "Habitat prope Vallisoletum et Irapaeum. Floret Novembri—Lex." The type has not been seen. "Irapaeum" is probably Uruapan (del Progreso) in Michoacán. The description is not sufficiently clear to enable positive identity with the north Mexican population. The actual type locality may be within the range of ssp. *lanceolata.*

The next available name, *macrantha,* also exhibits difficulties, for the type is a Sessé & Mociño collection. The type has not been seen but a photograph at Chicago and a Sessé & Mociño sheet at the Gray Herbarium yield no locality data. According to Hemsley (Jour. Bot. n. s. 8:275. 1879), Drs. Parry and Palmer later collected in the State of San Luis Potosí in essentially the same region as did Mociño & Sessé. The exact locality is still uncertain but still may be somewhat outside the range of this subspecies.

The name *grandis* is avoided because of the possibility of confusion with *Gentiana grandis* H. Sm. (Anz. Akad. Wiss. Wien, math.-nat. Cl. 63:100. 1926).

Greene's name for which the type *Forrer 44* (UC) plus two isotypes (F, GH) have been seen and for which the locality is known is thus employed. *G. macrocalix* and *G. macrantha* are placed in synonymy provisionally.

Arizona in the Huachuca and Santa Rita mountains, in the Sierra Madre of Chihuahua south to Durango and Zacatecas at altitudes of 2000–2600 meters; in moist areas and roadsides, steep open slopes, and in open pine forest; flowering from September until late November.

UNITED STATES:
ARIZONA: Cochise Co.: Huachuca Mts., *Lemmon 2823* (PH, US), *2883* (GH); Fort Huachuca, *Wilcox 489* (US). Santa Cruz Co.: Santa Rita Mts., *Peebles & Harrison 2955* (US), *Wooton s. n.* (US).

MEXICO:
CHIHUAHUA: *Palmer 361* (GH, NY, US); Santa Brigida, *Hewitt 88* (GH); Sierras near Huajochic, *Lumholtz s. n.* (GH); Sierra Madre, Mound Valley, *Jones s. n.* (US); near Guachochi, *Goldman 173* (GH, US); San Julian, *Nelson 4942* (GH, US); Memolichi, Rio Mayo, *Gentry 2726* (F, GH, MO, UC); 10 mi. s.e. Colonia Garcia, *Townsend & Barber 320* (F, NY); south Chihuahua, *Zingg s. n.* (F).

DURANGO: Sierra Madre, west of Durango, *Forrer 44* (F, GH, UC); Rosilla, *Collins & Kempton s. n.* (US); El Salto, *Martinez s. n.* (F).

SONORA: *Wright 1658* (GH, MO, NY, PH, US); Batocomori and Santa Cruz, *Thurber 926* (GH, NY).

ZACATECAS: Sierra de Valparaiso, *Goldman 6* (GH, US).

LOCALITY UNKNOWN: *Sessé & Mociño 685, 1371* (F), *s. n.* (GH, photo F).

1g. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. **lanceolata** (Benth.) J. M. Gillett, comb. & stat. nov.

Leianthus lanceolatus Benth. Pl. Hartw. 24. 1839. (T.: *Hartweg 209*!)
Gentiana lanceolata (Benth.) Griseb. in DC. Prod. 9:102. 1845.

Mexico from perhaps southwestern Chihuahua in the Sierra Madre to Michoacán, and in Vera Cruz about Cofre de Perote; altitude unknown; flowering from early September to late November; fruiting during November and December.

MEXICO:

JALISCO: Bolanos, *Hartweg 209* (GH, photo DAO, MO).

GUANAJUATO: *Duges 27* (GH).

MICHOACAN: Patzcuaro, *Pringle 3941* (F, GH, MO, NY, US); Morelia, *Arsène s. n.* (US).

SINALOA: Cueva del Diablo, *Dehesa 1562* (US).

ZACATECAS: Sierra de los Morones, Plateado, *Rose 2716* (F, GH, NY, US).

Subspecies *lanceolata* is distinguished chiefly by the entire corolla lobes, relatively slender flowers, and linear leaves. In Zacatecas, where the range overlaps that of ssp. *superba*, the flowers are larger and leaves broader. Since the material at hand is scant and extremely variable, it is difficult to elaborate further on this apparently clinal effect. However, such observations as have been possible indicate a low genetic barrier separating these two subspecies. The north-south trend of variation and the overlapping range seem to justify the recognition of this population merely as a subspecies of *G. detonsa.*

Mention should be made of a specimen collected by E. K. Balls (*5438*, US!) from Cofre de Perote, Vera Cruz. This specimen has shorter, more linear leaves than the other specimens of ssp. *lanceolata* and the corolla is more narrowly funnelform and attenuate to the pedicel. One interesting feature is the habitat, which Balls describes as: "bog, among rushes, etc." Since the slight morphological difference may be due only to environmental conditions, and because the range of variability is high in this group, no taxonomic recognition is given here to this collection.

1h. GENTIANELLA DETONSA (Rottb.) G. Don, ssp. **holopetala** (A. Gray) J. M. Gillett, comb. & stat. nov.

Gentiana serrata Gunn. var. *holopetala* A. Gray, Bot. Calif. 1:481. 1876. (T.: *Bolander 6359*!)
Gentiana holopetala (A. Gray) Th. Holm, in Ottawa Nat. 15:110. 1901.

Sierra Nevada Mountains in open wet meadows, hillsides, gravelly places and about springs in the Canadian and Hudsonian life zones, at altitudes of 2600–3300 meters; flowering from early July until about the end of August; fruiting in late August until the middle of September.

UNITED STATES:

CALIFORNIA: Calaveras Co.: Murphy's, *Lemmon 1137* (GH). Fresno Co.: Silver Pass, *Grant 1516* (MO). Inyo Co.: Cottonwood Lakes, *Alexander & Kellogg 3324* (GH, MO). Madera Co.: Upper San Joaquin, *Congdon s. n.* (MO). Mariposa Co.: Sierra Nevada, *Bolander 6359* (GH, MO, US). Mono Co.: Bloody Cañon, *Chesnut & Drew s. n.* (US); Sonora Pass, *Wiggins 9522* (CAN, GH, WS). Mono-Madera Cos.: Yosemite Nat. Park boundary, *Evans s. n.* (F). Placer Co.: Lake Tahoe region, *Smith s. n.* (F). Plumas Co.: *Austin s. n.* (GH). Sierra Co.: *Lemmon s. n.* (GH, PH). Tulare Co.: Nat. Bridge Meadow, *Culbertson 4260* (GH, F, MO); South Fork, Kern River, *Rothrock 313* (MO, PH, US). Tuolumne Co.: Tuolumne Valley, *Brewer 2847* (MO, US).

NEVADA: Boat Corral, *Coville & Funston 85* (US).

Gentianella detonsa ssp. *holopetala* is easily recognized by the long gynophore, entire corolla lobes, and the usually acute cauline leaves. Since these characters are variable, it seems advisable to consider the Californian population at a rank lower than species. Furthermore, occasional specimens superficially are very similar to specimens of subspecies *detonsa* from Alaska. The one Nevada collection seen resembles ssp. *elegans*, so that these subspecies may also intergrade. The Nevada collection lacks adequate data to enable it to be plotted.

An interesting character of ssp. *holopetala* is the almost hyaline wedges in the corolla tube below the sinuses, which in many herbarium specimens appear to be somewhat slack, rather suggesting the plicae between the lobes in *Gentiana*. For this reason many collections have been misidentified as *Gentiana newberryi* Gray. However, the "plicae" of ssp. *holopetala* are vascularized; those of *Gentiana* are not.

In his flora, Jepson[54] cited the type of *holopetala* as *Brewer 2847*. Gray, however, cited Bolander as the collector but gave no collection number. Bolander had a collection number *2847*, so that Jepson's error may have been due to a confusion of the names of the collectors. This plant is the dwarf plant mentioned by Gray; the Yosemite plant *(Bolander 6359)* is more typical and was also cited by Gray. To avoid further confusion, I consider this latter specimen, *Bolander 6359*, as the type.

2. GENTIANELLA CRINITA (Froel.) G. Don, Gen. Syst. 4:179. 1838.

Gentiana crinita Froel. Gent. Diss. 112. 1796, ex char.

Annuals (biennials or winter annuals?), 1–6 dm. tall, branched from the base or above, or simple. Basal leaves lingulate to spatulate, the apex rounded, obtuse or acute, the base attenuate to the stem, 0.8–1.6 (–3.3) cm. long, 0.1–0.6 (–1.0) cm. wide, soon withering or deciduous; median leaves linear, linear-oblong, lanceolate-ovate to ovate, elliptic in small forms, usually acute, the base attenuate to the width of the stem, or rounded or subcordate and clasping, 1.0–8.0 cm. long, 0.1–2.0 cm. wide. Flowers few to very numerous, or solitary, the terminal pedicels

[54] Jepson, Fl. Calif. 3^1:88. 1939.

2–22 cm. long, those of the branches usually shorter. Calyx narrowly to broadly funnelform, the tube 8–15 mm. long, 5–15 mm. wide below the sinus, the inner lobes ovate-triangular, subulate to acute, the outer lobes longer, lanceolate and conduplicate, the margins frequently carinate near the tip, acute, longer than or equal to the inner lobes; keels 0.7–1.0 mm. wide, scarcely to strongly prominent, weakly to strongly papillose (under magnification), dark green to purple-tinged; sinal membrane slightly to strongly curved and bearing few to many blunt processes up to 0.3 mm. long. Corolla pale to deep blue, rarely white, narrowly to broadly funnelform, 25–60 mm. long, 8–15 mm. wide at the orifice, the lobes oblong to obovate-oblong, the tips denticulate to short (1 mm.)-ciliate, the margins with fimbriae to 5 mm. long in the upper half. Stamens included, the filaments inserted in the lower third of the corolla tube, the marginal wings 1.3–3.0 mm. wide at the base, tapering above, strongly incurved; anthers 2–5 mm. long, about 1.5 mm. wide, attached in the upper third; interstaminal glands oval to rounded, prominent and frequently deep green. Pistil sessile to short-stipitate, the gynophore 2–4 mm. long, becoming obscure with age, ovary fusiform, 12–25 mm. long, 2–5 mm. wide; stigmas rounded to flabelliform or reniform, 1–3 mm. wide. Capsule as long as the corolla, dehiscing in the upper third, the tips of the valves slightly recurving. Seeds oblong and angular, light brown, the surface covered with rounded to elongate inflated brown papillae, particularly concentrated at the angles and ends.

North American, extending from the Appalachian Mountains and the Gulf of St. Lawrence in the east to the Great Lakes region and westward across the plains to the Rocky Mountains in Alberta, resolving into several intergrading subspecies apparently of a clinal nature and with numerous minor local variants.

Habitats various according to the subspecies, but in general preferring alkaline areas of about pH 6.7; flowering and fruiting roughly from June to late September; at usually low altitudes from sea-level to a few hundred meters.

Froelich provided an adequate description of *Gentiana crinita* but cited no specimens. In synonymy *Gentiana ciliata* L. (Syst. Pl. 1:645. n. 27) "α var. *americana*" is given. By "var. *americana*" Froelich apparently referred to the American element from which Linnaeus drew his description. At this time the problem of selecting a type is deferred because of the difficulty of obtaining certain literature and photographs. Because Fernald[55] interpreted the American portion of the *Gentiana ciliata* L. (Sp. Pl. ed. 2, 334. 1762) to be his *G. victorinii*, the difficulties are increased.

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[55] Fernald in Rhodora 25:85–89. 1923.

KEY TO THE SUBSPECIES

a. Flowers 25–60 mm. long; corolla lobes with lateral fringes 2–5 mm. long in the upper half of the lobe, the tips frequently short-ciliate also; calyx keels 0.1–0.8 mm. broad at the base.
  b. Median leaves ovate to lanceolate-ovate, rounded to subcordate at the base, linear to elliptic only in the small phase. North Carolina to Massachusetts and Maine west to Minnesota and Manitoba........2a. *G. crinita* ssp. *crinita*
  bb. Median leaves linear to linear-lanceolate. Upper New York through the Great Lakes region to Minnesota and Manitoba........2b. *G. crinita* ssp. *procera*
aa. Flowers 10–40 mm. long; corolla lobes with short lateral fringes, the tips dentate or erose, rarely ciliate; calyx keels absent or not prominent.
  c. Flowers 30–35 mm. long; corolla lobes orbicular; style 1.0–1.5 mm. long; stigmas flabelliform. Intercotidal zone of the St. Lawrence River. Quebec.....2c. *G. crinita* ssp. *victorinii*
  cc. Flowers 25–40 mm. long; corolla lobes usually oblong, somewhat truncate; stigmas reniform, sessile. Gaspé, Quebec, and James Bay, southward to North Dakota, westward to Alberta........2d. *G. crinita* ssp. *macounii*

The subspecies of *G. crinita* overlap in distribution a great deal so that many individual collections at the margins of ranges are difficult to assign. A general clinal condition exists between Alberta and the Appalachians. The eastward extreme has ovate to ovate-lanceolate leaves, long lateral corolla lobe fringes, long corollas, long-papillose seeds, coarsely papillose calyx keels, relatively distinct gynophores, and stems branching in the upper part. The western population consists of slender plants with linear leaves, shorter lateral fringes, small corollas, short seed papillae, less papillose keels, sessile capsules, and the stems branch chiefly from the base. Although no sharp division exists there is a change along certain lines that is useful for separation into subspecies. On the east side of the cline, ssp. *procera* differs from ssp. *crinita* principally in its linear leaves, although the flower characters seem to remain much the same. Other characters change gradually to merge with the plains subspecies. The western ssp. *macounii* is reserved for the short-flowered members, although occasionally long-flowered individuals appear. The key, of course, should be regarded as a guide only.

2a. GENTIANELLA CRINITA (Froel.) G. Don, ssp. CRINITA

Gentiana ciliata L. Syst. 1:645. 1756, in part, as to American element.
Gentiana fimbriata Andr. Bot. Rep. 509. 1808, ex ic.
Denckea crinita (Froel.) Raf. in Med. Repos. II. 5:352. 1808.
Anthopogon incarnatum Raf. New Fl. N. Am. 4:90. 1836, ex char.
Anthopogon brevifolium Raf. loc. cit. 91. 1836, ex char.
Gentiana crinita Froel. f. *albina* Fern. in Rhodora 19:152. 1917. (T.: *Bergen s. n.*!)

In the Appalachians from western North Carolina to Massachusetts and Maine, northwest to eastern Ontario and western Quebec, west to the Great Lakes region, forming a cline with *G. crinita* ssp. *procera* and with ssp. *macounii*, and occurring as far west as Minnesota and Manitoba.

In a variety of habitats: roadsides, clearings in open woods, swampy ground, gravel, sand, railway embankments, and shallow soils over limestone, in general preferring calcareous habitats. In the western part of the range found in open oak woods, on damp prairies, and boggy places; flowering throughout August to early October; fruiting from about mid-September until late October.

CANADA:

MANITOBA: Ochre River, *Groh s. n.* (DAO); Stony Mountain, *Groh s. n.* (DAO, MO), *Macoun s. n.* (CAN, F); Beausejours, *Schaeffer s. n.* (PH); Burnside, *McMorine s. n.* (DAO); Clear Lake, Riding Mt. Nat. Park, *Jackson 29–18* (DAO); Winnipeg, *Fowler 1* (DAO); Dauphin, *Scoggan 10503* (CAN); Grand Rapids, Lake Winnipeg, *Scoggan 4822* (CAN); Vivian, *Löve 5265* (CAN, JBM).

ONTARIO: Bruce Co.: *Bassett & Mulligan 194* (DAO). Carleton Co.: Britannia, *Macoun s. n.* (CAN, GH); Ottawa, Dow's Swamp, *Gillett 6055* (DAO), *Kellett s. n.* (CAN, DAO, MO); Kinburn, *Gillett 6056* (DAO); Lanark Co. border: *Dore & Gillett 47-1018* (DAO); Harwood Plains, *Dore & Rhodes 12868* (DAO). Elgin Co.: St. Thomas, *Fisher s. n.* (MO). Essex Co.: Turkey Point, Lake Erie, *Soper 759* (DAO). Grenville Co.: Merrickville, *Terrill 53* (DAO). Middlesex Co.: London, *Burgess s. n.* (CAN, DAO). Peterborough Co.: Clarina, Dummer Twp., *Dore & Hammond 14062* (DAO). Stormont Co.: Farran Point, *Dore & Van Rens 15667* (DAO). Waterloo Co.: Galt, *Herriot s. n.* (CAN, DAO); German Mills, *Montgomery 298.39* (DAO). Welland Co.: Niagara Falls, *McCalla 314* (CAN); St. Davids, *Scott 123* (CAN). Wentworth Co.: Hamilton, *Cody 105* (DAO). York Co.: Toronto, *Pennell 13124* (PH).

QUEBEC: Huntingdon Co.: Huntingdon, *Raymond & Kucyniak 2* (DAO, JBM).

UNITED STATES:

CONNECTICUT: Fairfield Co.: Stratford, *Eames s. n.* (GH). Hartford Co.: Southington, *Bissell 146* (MO). Litchfield Co.: South Canaan, *Greenman 1446* (GH, MO, US). Middlesex Co.: Saybrook, *Kennedy s. n.* (GH). New Haven Co.: New Haven, *Safford 259* (US).

ILLINOIS: Cook Co.: *Babcock s. n.* (US); Chicago, *Blankford s. n.* (F). Lake Co.: Waukegan, *Earle s. n.* (US). Stephenson Co.: Freeport, *Johnson s. n.* (US)

INDIANA: Allen Co.: Lake Everett, *Deam 22064* (GH). La Grange Co.: Ontario, *Deam 15057* (GH). Lake Co.: Clarke, *Lansing 3970* (F, GH). Porter Co.: Dune Park, *Chase 2115* (F, US), *Gillett 6058* (DAO). St. Joseph Co.: *Churchill s. n.* (MO); Chain Lakes, *Nieuwland 11650* (MO, US). Steuben Co.: Graveyard Lake, *Deam s. n.* (MO, US).

IOWA: Allamakee Co.: Postville?, *Schutz 182* (GH). Johnson Co.: *Fitzpatrick & Fitzpatrick s. n.* (F, GH, NY).

MAINE: Cumberland Co.: Falmouth, *Blake s. n.* (PH); Cape Elizabeth, *Gayle 904* (US); South Harpswell, *Keller s. n.* (PH); West Harpswell, *Read 3492* (MO). Kennebec Co.: Litchfield, *Sturtevant s. n.* (MO). Lincoln Co.: Monhegan Island, *Churchill s. n.* (MO). Oxford Co.: Hartford, *Parlin s. n.* (GH). York Co.: Kennebunkport, *Gilbert s. n.* (GH).

MARYLAND: Baltimore Co.: *Gresham s. n.* (US), *Morris s. n.* (PH).

MASSACHUSETTS: Berkshire Co.: Cheshire, *Churchill s. n.* (GH). Hampshire Co.: Worthington, *Rice s. n.* (US). Bristol Co.: Nonquit, *Sturtevant s. n.* (MO). Essex Co.: Bowford, *Murdoch 5264* (F). Franklin Co.: Buckland, *Forbes s. n.* (GH). Hampden Co.: West Granville, *Seymour 362* (GH, MO). Hampshire Co.: Mt. Tom, *Johnson 124* (US). Middlesex Co.: Chelmsford, *Beattie s. n.* (MO); Waverley, *Bergen s. n.* (GH). Norfolk Co.: Canton, *Kennedy s. n.* (GH). Plymouth Co.: Kingston, *Ridler s. n.* (F). Suffolk Co.: Boston, *Faxon & Faxon s. n.* (GH). Worcester Co.: Bolton, *Churchill s. n.* (GH, US).

MICHIGAN: Berrien County: *Millspaugh 3874* (F). Gratiot Co.: Alma, *Davis s. n.* (US). Jackson Co.: *Camp & Camp s. n.* (F). Midland Co.: Midland, *Dreisbach 5418* (PH). Washtenaw Co.: Geddes, *Farwell 7694* (GH). Wayne Co.: Dearborn, *Chandler s. n.* (US).

MINNESOTA: Clearwater Co.: Mississippi headwaters, *Grant s. n.* (GH, PH). Fillmore & Olmsted Cos.: Chatfield, *Hale s. n.* (PH). Hennepin Co.: Fort Snelling, *Mearns s. n.* (US). Houston Co.: *Freiberg s. n.* (MO). Morrison Co.: *Sandberg 877* (US). Nicollet Co.: St. Peters River, *Geyer s. n.* (MO, US). Todd Co.: Philbrook, *Hotchkiss & Jones 498* (GH). Winona Co.: Stockton, *Holzinger s. n.* (US).

NEW HAMPSHIRE: Belknap Co.: Gilmanton, *Gilbreth s. n.* (GH). Cheshire Co.: Marlboro, *Rohmann 373* (GH). Grafton Co.: Franconia, *Kennedy s. n.* (GH). Hillsboro Co.: Pelham, *Knowlton s. n.* (GH). Rockingham Co.: Derry, *Batchelder s. n.* (MO).

NEW JERSEY: Bergen Co.: Tenafly, *Poggenburg s. n.* (GH). Cape May Co.: Ocean View, *Meredith s. n.* (GH). Essex Co.: Verona, *Lighthipe s. n.* (MO). Morris Co.: Lake Hapatcony, *Fisher s. n.* (MO, US). Somerset Co.: Watchung, *Moldenke 7377* (CAN). Sussex Co.: Egypt Mills, *Bartram s. n.* (PH). Union Co.: Summit, *Parker s. n.* (GH).

NEW YORK: Albany Co.: Albany, *Beck s. n.* (NY). Broome Co.: Glenwood Ravine, *Millspaugh s. n.* (F). Columbia Co.: Canaan, *Harrison 11* (US). Dutchess Co.: Clove, *Standley & Bollmann 12365* (US). Erie Co.: Buffalo, *Clinton s. n.* (PH). Jefferson Co.: Watertown, *Keyes s. n.* (US). Madison Co.: Merrillsville, *House 26205* (GH). Monroe Co.: Irondequoit Valley, *Riley 7018* (GH). Niagara Co.: Cascadilla Creek, *Townsend s. n.* (WS). Ontario Co.: Geneva, *Wing s. n.* (MO). Orange Co.: Black Rock Forest, *Raup 7949* (GH). Richmond Co.: Staten Island, Richmond West, *Dowell 4285* (MO). St. Lawrence Co.: Oswegatchie, *Phelps 776* (GH, US). Suffolk Co.: River Head, *Miller s. n.* (US). Tompkins Co.: Fall Creek below Varna, *Eames & MacDaniels 4827* (GH). Washington Co.: Tripoli, West Fort Ann, *Burnham s. n.* (GH). Westchester Co.: Lake Mohegan, *Pennell 9328* (PH).

NORTH CAROLINA: Macon Co.: Nantahala Mountains, *Huger s. n.* (NY).

OHIO: Erie Co.: Milan Township, *Moseley s. n.* (F). Lucas Co.: *Pontius & Bartley 1006* (US).

PENNSYLVANIA: Berks Co.: *Small s. n.* (F). Bucks Co.: Bridgeton, *Bright 11036* (WS). Centre Co.: Scotia, *Kelly & Kelly s. n.* (GH). Chester Co.: *Rothrock s. n.* (F). Delaware Co.: *MacElwee 1468* (GH). Erie Co.: Presque Isle, *Garber s. n.* (PH). Huntingdon Co.: Whipple Dam, *Wahl 1170* (GH, US). Lancaster Co.: Dillerville, *Long 33914* (GH). Luzerne Co.: Wilkes-Barre, *Thurston s. n.* (US). Monroe Co.: Pocono Summit, *Small s. n.* (F, PH). Montgomery Co.: Greenlane, *Shaeffer 279* (GH). Northhampton Co.: Flowertown, *Dowell 1014* (US). Philadelphia Co.: Wissahickon, *James s. n.* (GH). York Co.: Loganville, *Glatfelter 349* (MO). Wyoming Co.: Osterhout, *Glowenke 9370* (GH).

RHODE ISLAND: Providence Co.: East Providence, *Reynolds 0656* (GH).

VERMONT: Bennington Co.: Shaftsbury, *Knowlton s. n.* (PH). Rutland Co.: West Rutland, *Eggleston s. n.* (GH); Ira, *Eggleston s. n.* (F). Windham Co.: Whittingham, *St. John 421* (PH, US).

WEST VIRGINIA: Greenbrier Co.: Lewisburg, *Franklin s. n.* (GH).

WISCONSIN: Brown Co.: Fort Howard, *Shuette s. n.* (F, GH). Crawford Co.: Prairie du Chien, *Hale s. n.* (MO). Monroe Co.: Sparta, *Palmer 28466* (MO). Racine Co.: Racine, *Davis s. n.* (GH). Sawyer Co.: Hayward, *Gilbert & Gilbert s. n.* (GH). Walworth Co.: Lake Geneva, *Blatchford s. n.* (F).

Because *G. crinita* ssp. *crinita* has been observed and collected in the field, a brief description of its habitat and mode of growth is introduced here.

During September, 1951, a small colony near the village of Kinburn, Carleton County, Ontario, about 20 miles west of Ottawa, was kept under observation. The colony was restricted to an area about one-eighth of a mile long and a few hundred yards wide, and was further restricted to shallow soil over limestone. Plants were rather abundant, and grew in open *Thuja occidentalis-Populus tremuloides* woods. *Halenia deflexa* also was found here but was restricted to a slightly drier microhabitat situated in clearings in *Thuja* woods. This microhabitat was termed a "cedar glade" in contrast to the more open and wetter habitat of *G. crinita.*

In direct sunlight, corolla lobes of *G. crinita* were observed to spread at an angle of about 45° but were closed in shaded places. The color of the lobes varied from a purple-blue to slightly reddish. The only insects observed about the flowers were a few ants and flies although thrips were found within the corollas.

The frequency and distribution of small, depauperate individuals within this population were of particular interest; for such plants had not only been observed on herbarium sheets, but had been deliberately selected out and described as forms and varieties by early authors. These small plants are about 5–20 cm. tall, and usually bear a single flower considerably smaller than those of the well-developed individuals. Moreover, in comparison with well-developed plants, the leaves are smaller and elliptic rather than ovate. In our colony, small plants were scattered among larger plants without any apparent preference to microhabitat. No definite explanation can be given at this time for the occurrence of these plants, but it is suggested that they are seedlings produced by early-flowering individuals during the same year. They are of interest, too, because they also occur in populations of other taxa in various parts of the continent. Large numbers of them were seen in Yellowstone Park, Wyoming, interspersed within a population of *G. detonsa* ssp. *elegans*, particularly.

In an effort to determine their life span, large plants from this colony were tagged and observed again the following year. In this region they prove to be annuals. No over-wintering rosettes were observed.

2b. Gentianella crinita (Froel.) G. Don, ssp. **procera** (Th. Holm) J. M. Gillett, comb. & stat. nov.

Gentiana barbata β Browniana Hook. ex Macnab, in Edinb. New Phil. Jour. 19:62. 1835. (T.: *Macnab s. n.*, photo MO!).
Anthopogon virgatum Raf. Fl. Tellur. 3:25. 1837, ex char.
Gentiana procera Th. Holm, in Ottawa Nat. 15:111. 1901. (T.: *Dodge s. n.*!)
Anthopogon procerus (Th. Holm) Rydb. in Brittonia 1:94. 1931.
Gentianella procera (Th. Holm) Hiit. in Mem. Soc. Faun. Fl. Fenn, no. 25:77. 1950.

From upper New York through the Great Lakes region to Minnesota, North Dakota and Manitoba. Clinal in nature, closely resembling ssp. *crinita* in the eastern part of the range except for the narrower leaves, approaching ssp. *macounii* in the western part, with shorter cilia, more linear leaves, lax habit and smaller seed papillae. In the western part including those individuals with coarse stems and large flowers.

Canada:

manitoba: Aweme, *Criddle s. n.* (DAO, MO); Bird's Hill, Winnipeg, *Denike 1759* (DAO); Ciento, *Dore 9196* (DAO); Carroll, *Senn & Gordon 3129* (DAO); Ochre River, *Scoggan 10508* (CAN); Stony Mountain, *Macoun s. n.* (CAN, F).

ontario: Bruce Co.: Hay Bay, *Krotkov 7212* (GH). Gray Co.: Craigleith, *Victorin & Germain 49464* (GH, MO, US, WS). Huron Co.: Banks of the Maitland River, *Macnab s. n.* (BM, PH). Lambton Co.: near Sarnia, *Dodge s. n.* (type, CAN), *Dodge 7082* (MO); Sarnia, *Macoun s. n.* (CAN). Manitoulin Dist.: Manitoulin Is., *Sims s. n.* (DAO); Wolsley Lake, *Thompson s. n.* (UBC); Fishing Is., Lake Huron, *Macoun s. n.* (CAN); Whitefish Is., *Macoun s. n.* (CAN); Cockburn Is., Boom Pt., *Grassl 400* (NY); Centre Is., *Ogden 2395* (US); Manitowaning Is., *Ogden 2428* (US); Johnstones Harbour, *Macoun s. n.* (CAN). Simcoe Co.: Collingwood, *Victorin, Rolland & Meilleur 45073* (DAO, GH). Waterloo Co.: Galt, *Herriot s. n.* (DAO, MO).

United States:

illinois: Cook Co.: *Babcock s. n.* (MO). Du Page Co.: *Moffatt 508* (GH). Kane & Cook Cos.: Elgin, *Sherff 1986* (MO). Kane Co.: Kankakee, *Greenman 3538* (MO).

Lake Co.: Waukegan, *Smith 6050* (GH, MO). McHenry Co.: Ringwood, *Vasey s. n.* (PH). McLean Co.: Normal, *Vasey s. n.* (GH). Winnebago Co.: Fountaindale, *Bebb s. n.* (NY, PH).

INDIANA: Fulton Co.: Bruce Lake, *Deam 46341* (GH). Kosciusko Co.: Chapman Lake, *Friesner 23145* (DAO, WS). Lake Co.: Pine, *Chase s. n.* (GH). La Porte Co.: Mill Creek, *Friesner 14190* (NY). Marshall Co.: Lake Maxinkuckee, *Scovell & Clark 1436* (US). St. Joseph Co.: Chain Lake, *Nieuwland 11642* (MO). Wayne Co.: Webster's Crossing, *Nieuwland s. n.* (US).

IOWA: Cerro Gordo Co.: Mason City, *Shimek s. n.* (MO). Dickinson Co.: West Okoboji Lake, *Shimek s. n.* (GH, MO, US, WS). Emmet Co.: *Cratty s. n.* (PH). Palo Alto Co.: 5 mi. e. Ruthven, *Hayden 10191* (GH, MO, NY). Winneshiek Co.: Fremont Twp., *Shimek s. n.* (MO).

MICHIGAN: Alpena Co.: Alpena Point, Lake Huron, *Cain, Raymond & Kucyniak 936, 943* (JBM). Calhoun Co.: Albion, *Barr s. n.* (F). Charlevoix Co.: Beaver Island, Lake Michigan, *Gillman s. n.* (NY). Cheboygan Co.: Mackinaw City, *Hermann 7311* (F, MO, US, WS). Emmet Co.: Wilderness State Park, *Cain, Raymond & Kucyniak 600* (JBM). Ionia Co.: Hubbardston, *Wheeler s. n.* (US). Kalamazoo Co.: Lyons Lake, *Kenoyer 278* (F). Kent Co.: Grand Rapids, *Crozier s. n.* (US). Mackinac Co.: Scotty Bay, Lake Huron, *Ehlers 4905* (F, US). Oakland Co.: Orian Twp., *Chandler s. n.* (US). Schoolcraft Co.: Manistique, *Cain, Raymond & Kucyniak 565* (DAO, JBM). St. Clair Co.: Port Huron, *Dodge s. n.* (NY). Washtenaw Co.: Cavanaugh Lake, *Grassl 7745* (MO). Wayne Co.: Detroit, *Schott s. n.* (F).

MINNESOTA: Cass Co.: Big Thunder Lake, *Richards 356* (F). Clay Co.: Muskoda, *Ballard 3064* (GH). Clearwater Co.: Itasca Park, *Grant 3362* (GH, MO, US). Dakota Co.: Nichols, *Rosendahl 4757* (F). Hennepin Co.: Fort Snelling, *Mearns s. n.* (US). Ottertail Co.: Richdale, *Chandonnet s. n.* (MO). Pope Co.: Glenwood, *Taylor s. n.* (PH). Ramsey Co.: St. Paul, *Sheldon s. n.* (GH, WS). Stearns Co.: St. Cloud, *Dewart s. n.* (MO). Winona Co.: Winona, *Holzinger s. n.* (US).

NEW YORK: Monroe Co.: Genesee River, *Eaton s. n.* (NY). Niagara Co.: Niagara Falls, *Canby s. n.* (NY); Goat Island, Niagara, *Engelmann s. n.* (MO). St. Lawrence Co.: Pollys Creek, *Muenscher & Maguire 1315* (GH).

NORTH DAKOTA: Ransom Co.: Anselm, *Stevens 227* (F).

OHIO: Champaign Co.: Urbana, *McFarland 4507* (US). Clark Co.: Tremont City, *Leonard 2018* (US). Pickaway Co.: Deer Creek, nr. Williamsport, *Collector unknown* (NY). Ross Co.: Kingston, *Bartley & Pontius 766* (NY).

WISCONSIN: Brown Co.: Fort Howard, *Schuette s. n.* (US). Dane Co.: Madison, *Heddle 953* (F). Door Co.: Bailey's Harbour, *Fassett et al. 14825* (GH). Milwaukee Co.: *Lapham s. n.* (DAO, GH, MO). Racine Co.: *Hasse s. n.* (NY). Waukesha Co.: Delafield, *Larrabee s. n.* (GH).

2c. GENTIANELLA CRINITA (Froel.) G. Don, ssp. **victorinii** (Fern.) J. M. Gillett, **comb. & stat. nov.**

Gentiana victorinii Fern. in Rhodora 25:87. 1923. (T.: *Victorin 16073*!)

Quebec, restricted to the intercotidal zone of the St. Lawrence River from Deschambault to St. Jean Port Joli; flowering from late July through August until early September; fruiting from mid-August until mid-September.

CANADA:

QUEBEC: Bellechasse Co.: Berthier, *Fernald 2536* (CAN, GH); Beaumont, *Victorin & Rolland 43667* (DAO); St. Vallier, *Victorin, Rolland & Meilleur 45546* (GH). Levis Co.: Levis, *Collector unknown* (DAO); St. Romauld, *Victorin, Rolland & Meilleur 1338* (JBM). L'Islet Co.: St. Jean Port Joli, *Desmarais 1013* (JBM), *Calder 1384* (DAO). Lotbinière Co.: St. Antoine-de-Tilly, *Victorin, Rolland & Jacques 33696* (CAN). Montmagny Co.: Grosse-Île, *Rousseau 21057* (GH), Berthier en Bas, *Victorin, Boivin, Raymond & Kucyniak 3726* (MO, WS), *Rousseau 21050* (CAN). Montmorency Co.: Ile

d'Orleans, Sainte-Petronille, *Victorin & Rolland 49500* (GH), *Gillett & Van Rens 9704* (DAO); St. Laurent d'Orleans, *Gillett & Van Rens 9722*, St. Jean, *Gillett & Van Rens 9723*, eastern end of Ile d'Orleans, *Gillett & Van Rens 9724* (all DAO). Portneuf Co.: Deschambault, *Gillett & Van Rens 9668* (DAO); Neuville, *Gillett & Van Rens 9693* (DAO); Saint-Augustin, *Victorin, Rolland & Jacques 33868* (GH). Quebec Co.: Cap Rouge, *Victorin 16073* (GH, JBM), *Gillett & Van Rens 9696* (DAO), *Victorin, Boivin, Raymond & Kucyniak 3704* (CAN, DAO, GH, MO, WS). And many more sheets from the same or near-by localities.

One of the most distinctive features of this subspecies is its unique habitat described in such detail by Raymond[56] and Rousseau.[57] During the summer of 1955 a visit was made by the author to this area. Both sides of the St. Lawrence were visited and a circuit made of l'Ile d'Orléans. From my observations it is suspected that the plants are annuals although Raymond cautiously writes: "Toutes ces espèces sont annuelles ou bisannuelles." The water throughout the range is fresh but may be salt in the eastern part following persistent east winds. As a result of daily flooding by the tide, the plants usually are covered with debris or a film of mud. A cline in flowering time was observed extending downstream from Deschambault on the north shore to Berthier and Montmagny on the south shore where the plants were in fruit only. The small phase seen in other populations occurs here also but is less common.

Subspecies *victorinii* is morphologically somewhat intermediate between ssp. *procera* and ssp. *macounii* and may be considered as a possible ecological nothomorph stemming from the *macounii-procera-crinita* cline.

2d. Gentianella crinita (Froel.) G. Don, ssp. **macounii** (Th. Holm) J. M. Gillett, **comb. & stat. nov.**

Gentiana macounii Th. Holm, in Ottawa Nat. 15:110. 1901. (T.: *Macoun s. n.*!)
Gentiana detonsa Rottb. var. *tonsa* Lunell, in Bull. Leeds Herb. 2:7. 1908. (T.: *Lunell s. n.*!)
Anthopogon tonsum (Lunell) Rydb. in Bull. Torr. Bot. Club 40:463. 1913.
Anthopogon macounii (Th. Holm) Rydb. loc. cit. 463. 1913.
Anthopogon procerum Lunell (incorrectly attributed to Th. Holm by Lunell), var. *tonsum* Lunell, in Am. Midl. Nat. 4:507. 1916. (T.: *Lunell s. n.*!)
Anthopogon procerum var. *tonsum* Lunell f. *uniflorum* Lunell, loc. cit. 1916. (T.: *Lunell s. n.*!)
Gentiana gaspensis Vict. in Contr. Lab. Bot. Univ. Montréal 20:10. 1932. (T.: *Victorin, Rolland & Jacques 33751*!)
Gentiana tonsa (Lunell) Vict. loc. cit. 14. 1932.

Alberta, Saskatchewan, and Manitoba, southern James Bay, and in Gaspé, Quebec; southward in the Great Plains through North Dakota and Minnesota and transitional to *G. crinita* ssp. *procera* west of the Great Lakes.

About the margins of sloughs and along river banks and meadows, occasionally in sandy swales and calcareous bogs. Flowering from late June to late August, fruiting during August and into September.

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[56] Raymond, M., in Nat. Canad. 78:81–87. 1951.
[57] Rousseau, J., in Contrib. Lab. Bot. Univ. Montréal 23:1–7. 1932.

CANADA:

ALBERTA: Lees Creek, Cardston, *Macoun s. n.* (CAN, TYPE); Fort Pitt, Saskatchewan River, *Macoun s. n.* (CAN); Banff, *Macoun s. n.* (GH, MO), *McCalla 2175* (NY, US), *Sanson in 1899, Fletcher in 1898* (CAN); Red Deer, *Grospe* (?) (WS); Calgary, *Turner 3759* (CAN); Shaganappi, *Moodie 44* (F, NY); Jasper, *Scamman 3357* (GH); Grattan Creek, *Macoun & Herriot s. n.* (CAN, NY); Blindman River, *Budd 1839* (SWC); Bow River, *Macoun s. n.* (CAN, US); Fort Saskatchewan, *Turner 2720* (CAN, DAO); Edmonton, *Moss 2412* (GH); Macleod North, *Dixon 1533* (DAO); Lacombe, *Lindsay & Leggett 339* (DAO).

BRITISH COLUMBIA: Field, *Macoun s. n.* (CAN, NY).

MANITOBA: Aweme, *Criddle s. n.* (DAO); Bird's Hill, Winnipeg, *Denike 1567* (DAO); Grand Rapids, Lake Winnipeg, *Scoggan 4854* (CAN); Beulah, *Dennis s. n.* (DAO); Ochre River, *Groh s. n.* (DAO); Little Saskatchewan River, *Scoggan 4942* (CAN); Lake Winnipegosis to Cedar Lake, *Scoggan 4639* (CAN); Verden, *Groh s. n.* (DAO); Stony Mountain, *Macoun s. n.* (F); Duck Mt., *Halliday 90* (CAN); Broomhill, *Senn & Gordon 3116* (DAO); Shoal Lake, *Garton 3165* (CAN); Bellhampton, *Bolton s. n.* (SWC).

ONTARIO: Albany, James Bay, *Dutilly & Lepage 16224* (CAN, DAO, US); Moose Factory to Rupert House, *Drexler s. n.* (GH); Albany, *Lepage 30245* (CAN, JBM); Delta of Albany River, *Johansen 30* (CAN), *Spreadborough s. n.* (CAN); Moose River, Renison, Mile 156, *Hustich & Tuomikoski 24* (CAN); Attawapiskat, *Dutilly & Lepage 16355* (CAN).

QUEBEC: James Bay: Rupert House, *Macoun s. n.* (CAN). Bonaventure Co.: Bonaventure River, *Kucyniak, Victorin, Boivin & Raymond 4008* (CAN, DAO, GH, MO, US, WS), *Marie-Victorin et al. 33751* (CAN, GH, JBM, NY), *Scoggan 1231, 981* (CAN), *Raymond & Kucyniak 1939* (CAN).

SASKATCHEWAN: McKague, *Breitung s. n.* (DAO); Nipawin, *Breitung 5998* (DAO, MO), *354* (CAN); South Saskatchewan River, *Boivin & Breitung 6700* (DAO); Rose Valley, *Dubreuil s. n.* (DAO); Canora, *Carmichael 189* (DAO); Prince Albert, *Fraser s. n.* (DAO); Tramping Lake, *Macoun & Herriot s. n.* (GH, NY, MO); Algrove, *Ledingham & Russell 1365* (DAO); Sutherland, *Russell s. n.* (DAO); Whitewood, *Tinline & Russell S3922* (DAO); Riwei Hills Reserve, *Rowe 442* (DAO); Pike Lake, *Russell s. n.* (DAO); Saskatoon, *Fraser s. n.* (SWC); Elbow, *Campbell s. n.* (SWC), Cut Knife, *Campbell s. n.* (SWC); St. Louis, *Senn, Groh & Russell 2843* (DAO); Carleton House to Bear Lake, *Richardson s. n.* (GH); Prongua, *Mead & Russell S1235* (DAO); Beasant, Moose Jaw District, *Hudson 570* (DAO); Blackfoot Crossing, Bow River, *Macoun s. n.* (CAN).

UNITED STATES:

MONTANA: Teton River, *Scribner 154* (GH, PH, US).

NORTH DAKOTA: Benson Co.: Butte, *Lunell s. n.* (MIN, MO, NY, US). McHenry Co.: Towner, *Lunell s. n.* (MIN); *Wright s. n.* (NY). Rolette Co.: Gravel Lake, *Mabbott 485* (US).

Gentiana gaspensis has been included within ssp. *macounii* since the differences are such that they easily come within the range of variation of the remainder of the population. The Gaspé specimens have slightly smaller flowers and branch from the base. However, nearly identical material occurs along the southern shore of James Bay, although I lack the habitat data necessary to ascertain whether it is confined to the same brackish meadow habitat as in the Gaspé plants. One or two collections from Manitoba also are exceedingly difficult to separate from the Quebec specimens. The occurrence of such plants seems to provide further evidence of a link with the western prairie population.[58]

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[58] Some material from James Bay nears *G. detonsa* in gross morphology but the papillose calyx keel versus the smooth keel separates all but a few sheets examined. Still I feel that the papillose-keeled fringed gentians and the smooth-keeled group form two natural divisions that should be maintained at the specific level at least for the present.

Although the type collection of subspecies *macounii* comes from Cardston, Alberta, it is not typical of the majority of the population. Alberta material is more frequently branched from the lower part than Saskatchewan and Manitoba material. This characteristic must be considered a local variant within the population as a whole since other characters either are identical or come within the variation range of the subspecies.

3. GENTIANELLA **barbellata** (Engelm.) J. M. Gillett, comb. nov.

Gentiana barbellata Engelm. in Trans. Acad. Sci. St. Louis 2:216. 1862. (T.: *Parry 208*!)

Gentiana moseleyi A. Nels. in Bot. Gaz. 31:396. 1901. (T.: *Moseley A.293*!)

Anthopogon barbellatus (Engelm.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.

Acaulescent or caulescent perennials 5–15 cm. tall, from slender, fleshy, branched, horizontal rhizomes, the rhizome branches erect, 5–10 cm. long, becoming thickened towards the surface. Basal leaves oblanceolate, rarely linear, rounded or obtuse, gradually attenuate below, expanded and connate to clasping at the base, forming a membranaceous sheath enclosing the ends of the rhizome, 1.5–9.0 cm. long, 0.3–1.2 cm. wide; median leaves oblanceolate to linear, obtuse or rarely acute, attenuate to about the width of the stem at the base, connate or clasping, 2–6 cm. long, 0.5–1.0 cm. wide. Flowers solitary and terminal, sessile or short-pedicellate, the pedicels to 5 mm. long, or axillary at the node immediately beneath, the axillary flowers sessile or short-pedicellate, the pedicels 1–2 cm. long; terminal flower (and occasionally the axillary flowers) subtended by a pair of frequently colored, hyaline-margined, lanceolate to linear, bract-like leaves. Calyx funnelform, 11–25 mm. long, 5–10 mm. wide at the orifice; lobes triangular to lanceolate, equal, as long as or shorter than the tube, somewhat crispate near the acute tips, 2–5 mm. wide at the base; sinuses acute, covered on the inside by a small membrane bearing 1–6 minute blunt processes 0.5 mm. long. Corolla deep blue, greenish yellow within, narrow funnelform, 24–45 mm. long, 5–10 mm. wide; lobes oblong with obtuse to acute erose tips, spreading in flower, irregularly crumpled and persistent in fruit, as long as the tube or longer, 15–25 mm. long, 2–6 mm. wide, the lateral margins with setae 1–2 mm. long in the lower half, entire to dentate in the upper. Stamens slightly exserted; filaments inserted above the middle of the corolla tube, the barely incurved marginal wings 0.5 mm. wide at the base, tapering gradually above; anthers oval, 2 mm. long, 1.5 mm. wide. Pistil stipitate, the gynophore 4–5 mm. long; ovary ellipsoid, sharply attenuate at the base, 10 mm. long, 3 mm. wide; stigmas sessile, elliptical, 2 mm. wide. Mature capsule as long as the corolla tube, dehiscing in the upper third, the tips of the valves erect. Seeds somewhat obovoid, papillose.

Central Colorado; Wyoming in Sublette, Teton and Carbon counties in the Medicine Bow Range; Utah in the La Sal Mountains; New Mexico in Colfax, Taos and Rio Arriba counties; Arizona in the San Francisco Mountains; at elevations of 1,000–3,600 meters; on rocky, alpine and subalpine slopes, below timber line in

open coniferous forest, and occasionally in open wet meadows; flowering from mid-August until late September, fruiting from mid-September until snowfall.

UNITED STATES:

ARIZONA: Coconino Co.: San Francisco Mountains, *Knowlton 126* (US).

COLORADO: Boulder Co.: *Moseley A.293* (RM). Clear Creek Co.: Berthoud's Pass, *Engelmann s. n.* (F, MO); Gray's Peak, *Patterson 94* (GH, MO, NY, US), *Rydberg 2793* (NY), *Jones 800* (NY), *Snow s. n.* (F). Custer Co.: Sangre de Cristo Mts. near Westcliffe, *Eggleston 6316* (US). El Paso Co.: Gentian Dell, *Clements & Clements 214* (GH, MO, NY, US). Gunnison Co.: Taylor River, *Coulter s. n.* (US). Jefferson Co.: Smith Horn, *Greene 327* (GH). Lake Co. Twin Lakes, *Wolf & Rothrock 794* (GH, US). Larimer Co.: Mount Flora, Snowy Range, *Parry 208* (MO, US); Estes Park, *Clokey 3832* (NY). Mineral Co.: Wagon Wheel Gap, *Murdock 4876* (F, MO). Park Co.: Leadville Forest, *Eggleston 11975* (US); Mt. Harvard, *Clements 409* (NY). Saguache Co.: *Weber 3598* (WS). San Miguel Co.: Wilson, *Mason s. n.* (NY); Breckenridge, *Brandegee 253* (MO, NY); Pike's Peak, *Underwood s. n.* (NY). Location unknown: *Parry in 1872* (NY), *in 1873* (F), *Parry 440* (F).

NEW MEXICO: Colfax Co.: Baldy Peak, *Standley 14343* (US). Taos Co.: Costillo Pass, *Howell 200* (US).

UTAH: Grand Co.: Stenize Stellen, La Sal Mts., *Purpus 7032* (MO, US). Sanpete Co.: Summit of Heliotrope, above Mayfield, *Collector unknown* (NY).

WYOMING: Carbon Co.: Medicine Bow Mts., *Nelson & Nelson 1138* (MO, NY). Sublette Co.: Green River Lakes, Wind River Mts., Mutulse Creek, *Griffiths s. n.* (NY); Cliff Creek, *Curtis s. n.* (NY), *Ownbey 1129* (MO, WS); 25 mi. w. Big Piney, above Middle Piney Lake, *Meyer & Meyer 2365* (NY). Teton Co.: Crystal Creek Divide, *Murie 1052* (MO).

Gentianella barbellata is the only perennial species of the genus in North America. The flowers bear unique rows of cilia below the staminal insertion, somewhat comparable to the substaminal cilia in the related European perennial *Gentianella ciliata* (L.) Börner. The latter has caudate seeds, however, while in *G. barbellata* the seeds are papillose and ecaudate.

A B

Fig. 2. A, distribution of *Gentianella simplex* (circles) and of *G. barbellata* (black dots). B, calyx and corolla of *G. simplex* (left), actual size, and of *G. barbellata* (right), × about 7/8.

4. Gentianella **simplex** (A. Gray) J. M. Gillett, comb. nov.

Gentiana simplex A. Gray in Newberry, Bot. Rept. U.S. Pac. R.R. Surv. 63:87. 1857. (T.: *Newberry s. n.*!)
Anthopogon simplex (A. Gray) Rydb. Fl. Rocky Mts. 659. 1917.

Annuals, 5–35 cm. tall; stems simple, smooth or finely striate. Leaves in 2–6 pairs, somewhat fleshy, the basal leaves spatulate, soon withering, 5–15 mm. long, 1–6 mm. wide, the apex rounded to obtuse, the base connate, the median and upper leaves elliptic, ovate, or lanceolate, 5–20 mm. long, 2–5 mm. wide, the apex obtuse, the base clasping to connate, slightly decurrent. Flowers solitary, terminal on pedicels 2–15 cm. long. Calyx narrowly funnelform, 10–25 mm. long, 5–10 mm. wide at the sinuses; lobes equal, as long as the frequently crispate tube, 5–12 mm. long, 2–5 mm. wide at the base, the outer foliaceous and veiny, occasionally crispate, the inner foliaceous or frequently strongly crispate and recurved; sinuses acute, covered within by a small entire membrane. Corolla pale blue to violet, narrowly funnelform, 20–40 mm. long, 4–10 mm. wide at the orifice; lobes broadly spatulate with rounded to obtuse, erose to dentate tips, erect to slightly spreading at anthesis, 5–15 mm. long, 3–6 mm. wide; sinuses acute, the lateral margins entire or with a few fringes 0.5–1.0 mm. long. Stamens included; filaments inserted in the middle of the corolla tube, the flat to slightly incurved marginal wings 1.5 mm. wide at the base, tapering slightly above; anthers 2 mm. long and wide, attached in the upper third; interstaminal glands elongate, swollen, attached 1 mm. from the base of the tube. Pistil stipitate, the gynophore 7 mm. long; ovary ovate, sharply attenuate at the base, 12 mm. long, 6 mm. wide; stigmas sessile, laminate and minutely lobed, 4 mm. wide. Mature capsule slightly exceeded by the persistent corolla lobes, dehiscing for one-third to half its length, the tips barely parted. Seeds elongate, caudate at both ends, 0.5–1.0 mm. long, 0.01 mm. wide, the body ovoid, the testa reticulate.

Mountains of southern and southeastern Oregon to eastern California, northern and western Idaho and western Nevada; in open meadows, wet places, and bogs; at elevations of 1200–3000 meters; flowering from late July until mid-October; fruiting from late August until the end of the growing season.

United States:

california: Alpine Co.: Spurs, *Hansen 708* (MO). Butte Co.: Jonesville, *Copeland 440* (F, GH, MO, US). Fresno Co.: Sierra Nevada, Dinky Creek, *Hall & Chandler 570* (MO, US). Lassen-Plumas Cos.: Sierra Nat. Forest, Shuteye Mt., *Murdoch 2537* (US). Mariposa Co.: Yosemite, *Chesnut & Drew s. n.* (US). Mono Co.: Bast Lake, *Copeland s. n.* (US). Placer Co.: Squaw Valley, *Brewer 2153* (GH, MO, US). Placer-Eldorado Cos.: Lake Tahoe Region, Angora Lake, *McGregor 210* (US). Plumas Co.: Big Meadows, *Austin 488* (MO, US). San Bernardino Co.: San Bernardino Mts., Little Bear Valley, *Parish 1659* (GH, MO, WS). Shasta Co.: Lassen Butte Region, *Eastwood 1890* (GH, US). Sierra Co.: Little Truckee River, *Sonne 218* (MO, US). Siskiyou Co.: Mt. Shasta, *Cooke 17810* (WS); Mt. Eddy, *Smith 554* (US); Scott Mt., *Engelmann s. n.* (MO). Trinity Co.: Carrville, *Howell 12755* (GH). Tulare Co.: Sequoia Nat. Park, *Cronquist 2182* (MO). Tuolumne Co.: Yosemite Nat. Park, *Van Schaack & Freytag 3055* (MO).

idaho: Boise Co.: Stanley, *Cronquist 3661* (GH, MO); Stanley Lake, *Christ s. n.* (ID). Boise National Forest, *Gillett, Senn & Frankton 6045* (DAO). Custer Co.:

Stanley Lake, Challis Nat. Forest, *Thompson 13971* (GH, MO, US); Cape Horn, *Macbride & Payson 3638* (GH, MO, US).

NEVADA: Washoe Co.: Incline, Lake Tahoe, *Mason 12208* (CAN, F, GH, MO, US, WS), *Archer 6714* (NY).

OREGON: Baker Co.: Eagle Creek Meadows, *Cusick 2336* (GH, MO, US, WS). Crook Co.: Ochoco Nat. Forest, *Munson & Bray 194* (WS). Deschutes Co.: Deschutes River, Tumalo Village, *Whited 548* (WS). Douglas Co.: Diamond Lake, *Coville & Applegate 460* (US). Klamath Co.: Lake of the Woods, *Applegate 321* (GH); Upper Klamath Lake, *Newberry s. n.* (MO). Umatilla Co.: *Mottet & Peterson s. n.* (ID)

A very distinct species. The height of this handsome plant is rather variable. Apparently this variability depends on the dryness of the habitat and on the nature of the surrounding vegetation. The living plant has been observed in the field in Boise National Forest, Idaho. Here, hundreds of plants in all stages of development grew in damp sandy ground among sedges and among scattered seedling pines. The plants were checked carefully for any deviation from the unbranched habit, and none was found. No insect visitors were seen about the plants, but dissections of several corollas revealed the presence of thrips. *Gentiana calyosa* growing near by was visited by both bees and humming birds.

Gentianella simplex may be related to *G. ciliata* of Europe. The caudate seeds of the two species are almost indistinguishable, and are unique among the fringed gentians. *G. ciliata*, however, is reported to be a perennial.

DOUBTFUL SPECIES

GENTIANA VENTRICOSA Griseb. Gen. & Sp. Gent. 259. 1839, is figured in Hooker's 'Flora Boreali-Americana' and may prove to be of considerable cytological interest. I am assured by Dr. N. Y. Sandwith that no photograph of the type specimen (*Drummond s. n.*, K: "ad cataractas fl. Saskatchewan terrarum Hudsons Bay") could add much to Grisebach's plate. Recently Dr. H. Scoggan of the National Museum of Canada collected another specimen of the same aspect at Grand Rapids, Lake Winnipeg, Manitoba (*Scoggan 4407*, Aug. 6, 1948, CAN!). These specimens have the ovary and stamens shorter than normal and the corolla is poorly developed. Apparently they do not form a large population but are found singly. It is suggested that the two polyploid series of different base numbers occasionally may hybridize to produce this sterile hybrid. That both Scoggan's and Drummond's specimens were collected in essentially the same region seems to indicate some cytological explanation for their occurrence. No similar oddities have been reported elsewhere in the group.

GENTIANA CRINITA Froel. β CERVANTESII Griseb. in DC. Prod. 9. 102. 1845—The type, a Cervantes collection, has not been located and the description of this Mexican entity is too brief for proper interpretation.

Subgenus II. Gentianella

Gentiana L. subgen. *Gentianella* (Moench) Kusnez. in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 4[2]:85. 1895.

SECTION AMARELLA (Gaudin, ex Griseb.) J. M. Gillett, comb. nov.

Gentiana § *Amarella* Gaudin, ex Griseb. Gen. & Sp. Gent. 238. 1839.

Flowers 4- to 5-merous, small. Calyx lobes with green margins, rarely reduced to teeth; sinuses without an inner membrane. Corolla 4- to 5-, rarely 6- to 8-parted, the lobes ovate, triangular or oblong, entire, the orifice with or without vascularized fimbriae, interstaminal glands epipetalous, and solitary. Stamens inserted near the middle of the tube or below; anthers oblong, slightly longer than wide; filaments glabrous. Ovary with the placenta confined to the sutures, rarely with an extra row of ovules along the ovary wall between the sutures. Seeds smooth, round to slightly flattened. Probably tetraploids on the base number nine.

KEY TO THE SERIES AND SPECIES

a. Corolla orifice usually naked, without faucal fimbriae, or fimbriate and the calyx spathe-like....................Series I. ARCTOPHILAE

- b. Calyx split to the base along one side to form a membranaceous spathiform sheath, the lobes reduced to green, apical teeth. Southeastern Arizona, western Chihuahua and Durango, Mexico....................5. *G. wislizeni*
- bb. Calyx tubular, the lobes well developed; orifice of the corolla always naked, with no trace of fimbriae at the base of the lobes.
  - c. Plants branched from the base or simple, the ascending basal branches frequently bearing reduced flowers.
    - d. Corolla lobes 4; outer calyx lobes broad and foliaceous; ovary narrowly ovoid to ellipsoid; flowers in loose simple cymes or axillary and solitary, occasionally in aggregate cymes, rarely subtended by a pair of bract-like leaves. Alaska and Canada south to Montana....................6. *G. propinqua*
    - dd. Corolla lobes 5; calyx lobes irregular but scarcely foliaceous; ovary generally broadly ovoid; flowers in compact terminal aggregate cymes or in a compact head due to reduction of the terminal internodes, subtended by the upper pair or pairs of bract-like leaves. Southwestern Greenland....................7. *G. aurea*
  - cc. Plants generally branched above, the flowers of the branches about equal to those of the main stem, not reduced.
    - e. Flowers perfect, about 2 cm. long; corolla lobes apiculate, half as long as the tube; calyx 4–10 mm. long. Maine to the southern Appalachians, westward to Minnesota, Missouri, and Arkansas....................8. *G. quinquefolia*
    - ee. Flowers occasionally polygamous, about 1 cm. long; corolla lobes obtuse to rarely acute, one-third to half as long as the tube; calyx minute, about 2 mm. long. Southeastern Arizona to Coahuila, Mexico....................9. *G. microcalyx*

aa. Orifice of the corolla with dense or scattered fimbriae at the base of the lobes....................Series II. AMARELLAE

- f. Corolla lobes as long as the tube; faucal fimbriae free, rather thick and blunt, somewhat hyaline; capsule with a few (6 or less) oblong seeds. Southwestern Utah to southwestern Nevada....................10. *G. tortuosa*
- ff. Corolla lobes shorter than the tube; faucal fimbriae slender, opaque; capsule with many ovoid seeds.
  - g. Calyx tube shorter than or equal to the acute to obtuse lobes; faucal fimbriae free at the base (united in ssp. *heterosepala*); terminal flowers about equal in length to the lateral ones. Labrador and Newfoundland to Maine and Vermont; westward to Alaska and southward in the mountains to Baja California; Black Hills; Rocky Mountains southward to central Mexico....................11. *G. amarella*
  - gg. Calyx tube longer than the rounded, frequently auriculate lobes; faucal fimbriae united at the base; terminal flowers larger than the lateral. Attu Island, Aleutian Islands, Alaska....................12. *G. auriculata*

Series I. ARCTOPHILAE J. M. Gillett, ser. nov.

Aloitis Raf. Fl. Tellur. 3:21. 1837. (T.: *A. quinquefolia* (L.) Raf.)
Gentiana L. sect. *Arctophila* Griseb. Gen. et Sp. Gent. 250. 1839.

5. Gentianella wislizeni (Engelm.) J. M. Gillett, comb. nov.

Gentiana wislizeni Engelm., in Trans. Acad. Sci. St. Louis 2:215. 1862. (T.: *Wislizenus 206*!)
Amarella wislizeni (Engelm.) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Annuals 1–5 dm. tall; stems prominently angled, branched above the base, the branches ascending. Basal leaves ovate, oblanceolate, elliptic to spatulate, 5–20 mm. long, 3–6 mm. wide, soon withering and frequently deciduous, occasionally forming a loose rosette; median leaves ovate to lanceolate, the apices obtuse in leaves of the lower third of the plant, becoming acute above, the base cordate and clasping, 15–35 mm. long, 5–15 mm. wide; upper leaves similar to the median but becoming progressively more lanceolate, the tips acute. Flowers axillary or terminal, in aggregate cymes, rarely in simple cymes or solitary, the flowers frequently secund or nodding; pedicels straight or strongly curved particularly when young, 3–20 mm. long. Calyx 4–6 mm. long, slit to the base along one side to form a membranaceous spathiform sheath partially enclosing the corolla, the lobes reduced to 4–5 minute, green teeth borne on the rim of the sheath. Corolla pale blue or white, tubular to narrowly funnelform, 6–13 mm. long, 2–4 mm. wide at the orifice, the lobes triangular-ovate, acuminate, one-fourth the length of the tube, very widely spreading, bearing at the orifice few to many ciliate fimbriae, or naked, the interfilamental glands distinct and swollen, more or less oblong-scutiform. Stamens slightly exserted, the filaments inserted near the middle of the corolla tube, the wings about 2.5 mm. wide at the base and tapering slightly above; anthers oblong, 0.8–1.1 mm. long, about 0.75 mm. wide, versatile and attached near the middle. Pistil subsessile or with a gynophore not exceeding 1 mm. long, the ovary linear-lanceolate, 7–8 mm. long, 1.0–1.5 mm. wide, stigmas sessile, oblong, 0.6 mm. long, 0.4 mm. wide, erect. Capsule longer than the marcescent corolla, up to 14 mm. long, dehiscing in the upper one-sixth, the valves recurving at the tip. Seeds ovoid, 0.75 mm. long, 0.5 mm. wide, distinctly flattened, the surface smooth, minutely wrinkled under high magnification, light brown.

In the White Mountains of Apache County and in the Chiricahua Mountains of Cochise County, Arizona; throughout the Sierra Madres of Chihuahua, and extending into Durango at altitudes of 2100–2500 m., on cool slopes and in stony pine woods; flowering throughout September and fruiting from late September until mid-October.

United States:

arizona: Apache Co.: White Mts., *Rothrock 799* (GH, MO, US). Cochise Co.: Chiricahua National Mon., Barfoot Park, Chiricahua Mts., *Blumer s. n.* (GH, NY, US), *177* (US), *Eggleston 10819* (GH, US); Rustler Park, *Jones 28730* (MO).

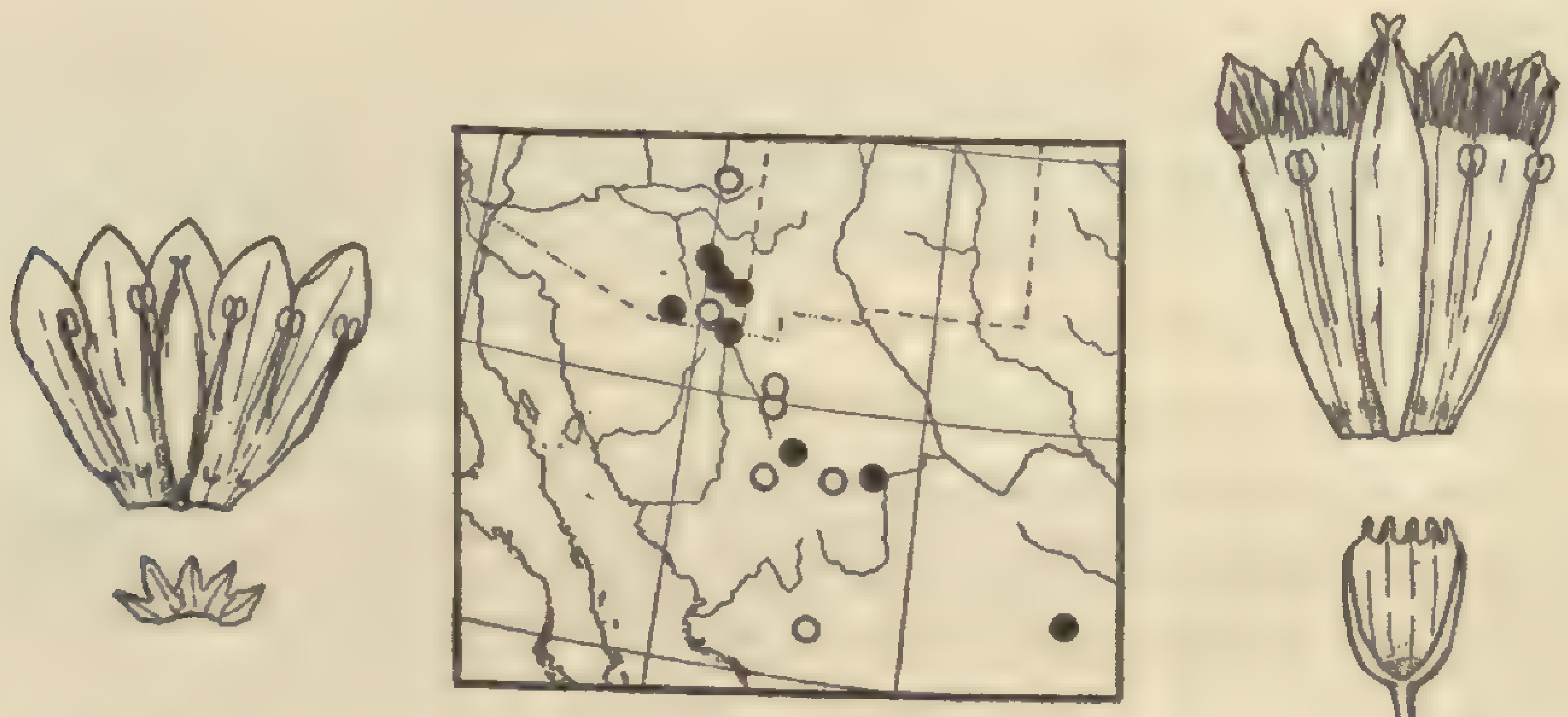
Mexico:

chihuahua: Sierra Madre, between Rio Chico and Rio Caballo, *Barlow s. n.* (F, US); Santo Domingo between Concheno and Pinos Altos, *Hewitt 78* (GH); Mesa west of Hop

Valley, *Jones s. n.* (US); *Pringle 1329* (F, GH, MEXU, NY, US), *1662* (MO, NY); near Colonia Garcia, *Townsend & Barber 322* (F, GH, MO, NY, US); *Collector unknown* (MO); *Pennell 19097, 19136* (US); Majarachie, *Knobloch 5614* (F); mountains of Llanos, *Wislizenus 206* (GH, MO).

DURANGO: road between San Julián and Cerro Pierto, *Nelson 4950* (US).

The distinctive spathiform calyx assures instant recognition of *G. wislizeni.* The fimbriate corona at the orifice of the corolla is extremely variable, ranging from a dense row of ciliate fimbriae extending entirely across the base of each lobe to completely lacking in a few specimens. The lack of correlation between geography and the occurrence of plants with naked corollas prohibits recognition of them as a distinct taxon. Even as the criterion for a sporadic form the feature fails, since both types of flowers have been found on the same plant. Engelmann placed this species in *Gentiana* sect. ARCTOPHILA, perhaps because of the lack of fimbriae in most specimens that he examined, although both fimbriate and naked specimens were apparently seen by him.



A B C

Fig. 3. A, calyx and corolla of *Gentianella microcalyx*, × 1½. B, distribution of *G. wislizeni* (black dots) and of *G. microcalyx* (circles). C, calyx and corolla of *G. wislizeni*, × 1½.

6. GENTIANELLA **propinqua** (Richards.) J. M. Gillett, comb. nov.

Gentiana propinqua Richards. in Frankl. Narr. 1st Jour. 734. 1823. (T.: *Richardson s. n.*, photo MO!)

Annuals 2–35 cm. tall, simple or branched from the base, the branches usually shorter than the main stem, curved-ascending, and bearing smaller flowers. Basal leaves frequently forming a dense rosette, elliptic to spatulate, the apex rounded to obtuse, gradually attenuate to the base, 5–35 mm. long, 2–8 mm. wide; median leaves ovate, ovate-elliptic to lanceolate, the apex acute to obtuse, the base generally broadened, rounded or clasping, 5–35 mm. long, 2–10 mm. wide; upper leaves similar to the median. Flowers 4-merous, axillary or terminal, in simple cymes or solitary, occasionally in aggregate cymes, the terminal flower conspicuously larger than the lateral ones or nearly equal in ssp. *aleutica*; pedicels 4–30 mm. long, the lateral flowers sessile or with pedicels correspondingly shorter. Calyx 5–12 mm. long, the tube 2–3 mm. long; lobes ovate to lanceolate, acute, the outer lobes wider than the inner, about twice as long as the tube, the margins minutely papillose-

toothed or entire, the sinuses acute. Corolla pale blue to white, tubular to narrowly funnelform, 12–20 mm. long, 3–5 mm. wide at the orifice, the lobes ovate to ovate-lanceolate, one-third to half the length of the tube, the tips mucronate or denticulate, the sinuses acute or more commonly concealed by the imbrication of the lobes, the orifice of the tube naked; interstaminal glands distinct, scutiform, and appearing as a pale green patch at or slightly above the base. Stamens included or slightly exserted, the filaments inserted about the middle of the corolla tube, the wings 0.25–0.50 mm. wide at the base and tapering slightly above; anthers oblong, 0.7–1.5 mm. long, 0.6–1.2 mm. wide, versatile and attached near the middle. Pistil very shortly stipitate, the gynophore 0.5 mm. long; ovary cylindrical, 7–10 mm. long, 1–2 mm. wide; stigmas sessile, elliptic, 1.25 mm. long, 0.4 mm. wide, erect. Capsule longer than the marcescent corolla, up to 25 mm. long, dehiscing in the upper fourth. Seeds ovoid, slightly flattened, 0.5–0.75 mm. long, 0.5–0.6 mm. wide, smooth, minutely wrinkled under magnification, light tan to dark brown.

Throughout Alaska and the Yukon on mountains and in valleys, extending through the Rockies to west-central Alberta and east-central British Columbia; from the Arctic Ocean occurring sporadically to the shores of Hudson Bay, with isolated stations in Beaverhead County, Montana, Gaspé County, Quebec, and the Straits of Belle Isle in Newfoundland; in a wide variety of habitats, such as alpine meadows, rocky shady hillsides, open sandy clay, gravel, or limestone areas, pine or mixed forests and in clearings, along streams and borders of marshes and in muskegs, on glacial moraines and on sea beaches, at altitudes from sea-level to about 3000 meters; flowering from mid-June until early September, fruiting from August until late September.

KEY TO THE SUBSPECIES

a. Terminal flowers 15–20 mm. long, conspicuously larger than the lateral; corolla lobes apiculate, blue. Newfoundland to Alaska south to Montana.........6a. *G. propinqua* ssp. *propinqua*

aa. Terminal flowers about 10 mm. long, about as long as the lateral flowers or slightly larger; corolla lobes obtuse and somewhat denticulate, pale violet to white. Aleutian Islands to southern Alaska..........6b. *G. propinqua* ssp. *aleutica*

6a. Gentianella propinqua (Richards.) ssp. propinqua

Gentiana rurikiana Cham. & Schlecht. in Linnaea 1:176. 1826, ex char. (T.: *Chamisso s. n.*)

Gentiana gracilis Cham. & Schlecht. loc. cit. 1826, nom. nud.

Gentiana setiflora Bunge, in Mem. Soc. Imp. Nat. Mosc. 7 (Nouv. Mem. Soc. Nat. Mosc. 1):242. *t. 9. fig. 4.* 1829, ex char. et icon.

Gentiana propinqua β densiflora Griseb. in Hook. Fl. Bor. Am. 2:62. 1838. (T.: *Drummond s. n.* photo MO!)

Gentiana arctophila Griseb. in Hook. loc. cit. 61. 1838. (T.: *Richardson s. n.*!)

Gentiana arctophila β densiflora Griseb. in Hook. loc. cit. 1838. (T.: *Drummond s. n.*!)

Amarella propinqua (Richards.) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Amarella arctophylla (Griseb.) Greene, loc. cit. 1904.

Amarella ventorum Rydb. in Bull. Torr. Bot. Club 40:463. 1913, ex char. (T.: *Fremont s. n.*?)

Newfoundland to Alaska and southward in the Rocky Mountains to western Montana.

United States:

alaska: Donnelly Dome, Mile 250, Richardson Highway, *Cody 6294* (DAO); Jarvis Creek, Mile 267, Richardson Hwy, *Cody & Webster 5957* (DAO); near Delta Junction, *Cody & Webster 6024* (DAO); Mile 36, Slana-Tok Hwy. *Anderson 8691* (CAN); Kobuk River, *Palmer 652* (F); Umiat, Colville River, *Spetzman 2100* (CAN); Ignek Valley, *Spetzman 1470* (CAN); Sadlerochit River, *Spetzman 1001* (CAN); White Mts., Sheep and Mascot creeks, *Gjaerevoll 389* (CAN); Bennett, *Cowles 994* (MO); Yukon River between Rampart and Tanana, *Palmer 17* (CAN); Kotzebue-Lund, *Eschscholtz s.n.* (MO); Nome, *Jones 9165* (MO); Eagle Summit, *Lepage 25381* (DAO); Savage River, *Mexia 2100* (DAO, MO); Mt. McKinley Nat. Park, Mile 66, *Nelson & Nelson 3978* (GH, MO, NY); Alaska Range, Nenana Valley, *Porsild & Porsild 367* (CAN, GH); Castner Glacier, *Porsild & Porsild 503* (CAN, GH); between Summit and McCarty, *Porsild & Porsild 439* (CAN, GH); Kokrines Hills above Yukon River, *Porsild & Porsild 681* (GH); Pastolik, Norton Sound, *Porsild & Porsild 1015* (CAN, GH); near Bluff, Seward Peninsula, *Porsild & Porsild 1269* (CAN, GH); Mile 189, Richardson Hwy., *Webster 121* (DAO); Fort Yukon, *Kennicott s.n.* (F).

montana: Beaverhead Co.: Sheep Mountain, *Hitchcock & Muhlick 12887* (MO, WS).

Canada:

alberta: Lake Louise, *Anderson s.n.* (CAN, WS), *Lasalle 45105* (CAN); Pabatac Creek, *Brown 1342* (MO); Vermillion Slope, *Fletcher s.n.* (DAO); Blair Mt., *Lambert s.n.* (CAN); Banff National Park, Bow Peak, *Hitchcock & Martin 7741* (plants #2, 5 GH, WS); near Banff, *Macoun s.n.* (MO); Sunwapta Pass, *Ledingham 49-605* (DAO); Wicked River, near Peace River, *Raup & Abbe 4331* (CAN); Smoky River, *Riley 35* (US); Jasper National Park, Mt. Edith Cavell, *Ledingham 49-627* (DAO); Miette Hot Springs, *Turner 5134* (DAO); Athabasca Falls, *Turner 6948* (CAN, DAO); Peyto Glacier, *Weber 2440* (WS).

british columbia: Mt. Pope, n.w. Ft. St. James, *Calder, Savile & Ferguson 13798* (DAO); Mt. Thornhill, near Terrace, *Calder, Savile & Ferguson 14839* (DAO); Murray Range, Azouzetta Lake, *Calder, Savile & Ferguson 14059* (DAO); Mt. McLean at Lillooet, *Calder, Savile & Ferguson 15517* (DAO); Yoho Mt., *Bostock s.n.* (DAO); Mt. Stephen near Field, *Calder & Savile 12038* (DAO); Field, Lake O'Hara, *Brown 951* (MO); between Field and Mt. Wapta, *Walcott s.n.* (US); Burgess Pass, *Fyles s.n.* (DAO); Marble Canyon, *Groh s.n.* (DAO); Kicking Horse Lake, *Macoun s.n.* (CAN, DAO, GH, US); Chilliwack Valley, *Macoun s.n.* (US); Bennett, *Cowles 994* (F); Chipuin Mt., Marble Mts., *Thompson & Thompson 558* (CAN, MO, NY, PH, US); Paradise Mine, Windermere, *Calder & Savile 11265* (DAO); Loggan, *Macoun s.n.* (F); Atlin Lake, *Aitken 21* (DAO); Tonquin Valley, Jasper Park, *Kindle s.n.* (CAN); N. Kootenay Pass, *Dawson s.n.* (CAN); Mt. Selwyn, *Raup & Abbe 4055* (CAN).

mackenzie district: Coppermine, *Findlay 240* (DAO); Dismal Lake, *Hall s.n.* (UBC); Bernard Harbour, *Johansen 372* (CAN, GH); Mackenzie River, *Onion, Kennicott & Hardisty s.n.* (PH); Bear Lake, *Richardson s.n.* (K type, GH); Thelon River, Hornby's Bend, *Tener 266* (CAN); Thelon Game Sanctuary, The Angle, *Clarke s.n.* (CAN); Camp Franklin, Great Bear River, *Lindsey 523* (CAN); Canol Road, Mt. Range, Bolstead Creek, *Wynne-Edwards 8363* (CAN); Mark River, Lone Mt. near the North Nahanni River, *Wynne-Edwards 8505* (CAN); Liard River betw. Nahanni Butte and Simpson, *Crickmay 99* (CAN); Great Bear Lake, Dease River Valley, *Porsild & Porsild 4878* (CAN); McTavish Arm, *Porsild & Porsild 5182* (CAN); Leith Point, *Porsild & Porsild 3588* (CAN); Great Bear River, jct. Big Stick River, *Porsild & Porsild 3270* (CAN); Eskimo Lake basin, Setidgi Lake, *Porsild & Porsild 3162* (CAN); Kugaruk, n. Anderson River, *Porsild & Porsild 3088* (CAN); Liverpool Bay, Nicholson Island, *Porsild & Porsild 2927* (CAN); Mackenzie River delta, Kittigazuit Island, *Porsild & Porsild 2390* (CAN); Campbell Lake, Point Separation, *Porsild & Porsild 1957* (CAN); Richardson Mts., *Porsild & Porsild 6847* (CAN); Mackenzie Bay, *Stringer s.n.* (CAN).

FRANKLIN DISTRICT: Banks Island, n. of Cape Lambton, *Porsild 17593* (CAN); Victoria Island, vic. Holman Is. Trading Post, *Porsild 17328* (CAN); Banks Island, Nelson Head, *Manning & Macpherson 112* (CAN).

MANITOBA: Churchill, *Gillett 2340* (DAO, MO), *Macoun s.n.* (CAN), *Polunin 40* (CAN), *Porsild 5494* (CAN); York Factory, *Bell s.n.* (CAN), *Scoggan 6052* (CAN).

NEWFOUNDLAND: Mistaken Cove, Straits of Belle Isle, *Fernald, Long et al. 26975* (F).

ONTARIO: Cap Henriette, *Dutilly & Lepage 31244* (DAO); Lake River, *Smith 86* (CAN); South Twin Island, *Johansen 274* (CAN).

QUEBEC: Gaspé Co.: Anse Pleureuse, *Victorin & Germain 49435* (DAO); James Bay: Cap Jones, *Dutilly, Lepage & Duman 32527* (DAO).

YUKON TERRITORY: Dawson, *Calder & Billard 3380* (DAO), *Eastwood 425* (F); 60-mile road, West Dawson to Alaskan border, *Calder & Billard 4418* (DAO); Mayo Lake, *Green 24* (DAO); Whitehorse, *Gillett 3463, 3470, 3660, 3813, 3834* (DAO); Keno Hill, *Gillett, Calder et al. 4338* (DAO); North Fork, Klondike River, *Cockfield 51* (CAN); Cassiar Mts. 20–30 miles e. Teslin Lake, *Poole s.n.* (DAO); Lake Laberge, *Gillett & Mitchell 3959* (DAO); Big Salmon, Lewes River, *Gillett & Mitchell 3971* (DAO); Stewart Landing, *Gillett & Mitchell 4084* (DAO); Independence Creek, Stewart River, *Gillett & Mitchell 4134* (DAO); Mt. Caribou, nr. Carcross, *Gillett & Mitchell 4568* (DAO); Rampart House, *Loan 681* (DAO); Coffee Creek, *Malte 44, 50* (CAN, GH); Reindeer Creek, Yukon River, *Barton s.n.* (UBC); Bear Creek, nr. Lake Desert d'Asch, *Müller s.n.* (MO); Snag, *Noel 43* (CAN, UBC); Mile 180, north of Fort Nelson, *Williams s.n.* (UBC); Mackintosh, Alaska Hwy., mile 1022, *Anderson & Brown 10053* (CAN); Moosehide Mt., *Campbell 51* (JBM); Frith River, *McEwan 194* (CAN); Canol Road, Mt. Sheldon, *Porsild & Breitung 11753* (CAN); Mile 132, Lower Lapie River Crossing, *Porsild & Breitung 9991* (CAN); Mile 95, Upper Rose River valley, *Porsild & Breitung 10403* (CAN); Mile 36–42, Misutlin River, *Porsild & Breitung 10849* (CAN); Herschell Island, *Johansen 559* (CAN); Franklin Expedition, *Richardson s.n.* (CAN).

LOCATION UNKNOWN: Arctic Sea Coast, *Richardson s.n.* (CAN, GH); Rocky Mts., *Drummond s.n.* (K, GH).

Gentianella propinqua ssp. *propinqua* is recognized easily by the larger terminal flowers, with apiculate corolla lobes. These features, coupled with the ascending basal branches, provide good field characters for distinguishing *G. propinqua* from *G. amarella* ssp. *acuta* where these species occur together.

This species has been examined in the field, particularly in the Yukon. The height of the plant varies considerably in the Whitehorse area, simple and branched plants growing side by side in habitats ranging from forests of *Pinus contorta* var. *latifolia* to open bare sandy places. Numerous dead plants from previous years were found in sheltered wet places, their condition clearly indicating their annual character. At Carcross, Yukon Territory, I had an opportunity to climb Mt. Caribou and to observe that the plants decrease in size with increase in altitude without any apparent break in the population continuity, except perhaps on rock slides where growth of plants in general was curtailed.

A journey by steamer along the Lewes and Stewart rivers revealed an almost continuous distribution between Whitehorse and Mayo Landing.

At Churchill, Manitoba, the species was not common and was restricted to gravelly roadsides and to the edge of the airport runways.

A few specimens from southern British Columbia and the solitary specimen from Montana have corolla lobes that are broadened above the sinus and bear no apicula at the tip (*arctophila* type). Except that they occur in this general region, there appears to be no definite boundary to the population. One sheet, *Calder & Savile 12038*, collected at an altitude of 7,700 feet on Mount Stephens near Field,

B. C., bears both apiculate and exapiculate plants. The sixteen plants on the DAO sheet are all quite small and were found on an open heath near talus slopes. The smallest plant is 3 cm. high and bears a flower fully 2 cm. long with obtuse exapiculate lobes; the largest plant is 6 cm. tall and has normal apiculate flowers indistinguishable from many other collections.

During the summer of 1954, J. A. Calder and D. B. O. Savile encountered a patch of pure white-flowered *G. propinqua* located not more than a few yards away from the blue-flowered form. Although white-flowered forms occur among most colored-flowered plants, these plants show a complete lack of the purple coloration normally present in *G. propinqua.* Probably this is an expression of a recessive character, but because a considerable colony had apparently become established within the blue-flowered population, I feel justified in providing it with a name.

GENTIANELLA PROPINQUA (Richards.) J. M. Gillett forma **acyanea** J. M. Gillett, form. nov.

Plantae viridulae non purpureo-tinctae; floribus in vivo albis in sicco ochroleucis.

CANADA:

BRITISH COLUMBIA: Steep slope at base of cliffs at 5,000 ft. near head of valley, Western Uranium Mine about 9 miles ne. of Skeena Crossing, Aug. 30, 1954, *Calder, Savile & Ferguson 1520A* (DAO, HOLOTYPE); rare in deep shade of spruce woods, acid habitat and in moss by spring in muskeg, Mile 250, Richardson Hwy. near base of Donnelly Dome, Aug. 2, 1951, *Cody 6294* (DAO).

The paucity of data available to me prohibits any correlation of the characters of *G. arctophila,* as given by Grisebach, with either geographic area or altitude. Until such data are available, it seems best to relegate this name to synonymy of *G. propinqua.* However, the following comments regarding the types of *G. arctophila* and *G. arctophila β densiflora* may be of interest, should the necessity arise to give the populations taxonomic recognition.

A sheet from the Gray Herbarium has four different collections, among which one is labeled "*Gentiana arctophila* m. B.N.A. nr. 17."; below this specimen, in another hand, appear the words "*R. Mts.* Hook." Above the label are three plants, one of which is separated from the others by a line and labelled "Arctic Sea-coast". In the New York Botanical Garden Herbarium, a Meisner Herbarium sheet is labeled "*Gentiana arctophila* Gr. America arctica" in the same handwriting as the name on the Gray sheet. On this same label in a different hand is the comment "Com. cl. Grisebach 28/4/65." These specimens compare very closely with the photographs of the type from Kew.

This evidence seems to indicate that the Gray sheet, at least, consists of isotypes of both *G. arctophila* and *G. arctophila β densiflora* and that they were collected as stated by Grisebach (Hook. Fl. Bor.-Amer. 2:62): "HAB. Arctic Sea-Coast. *Dr. Richardson.* β Rocky Mountains. *Mr. Drummond.*"

6b. GENTIANELLA PROPINQUA (Richards.) J. M. Gillett, ssp. **aleutica** (Cham. & Schlecht.) J. M. Gillett, comb. & stat. nov.

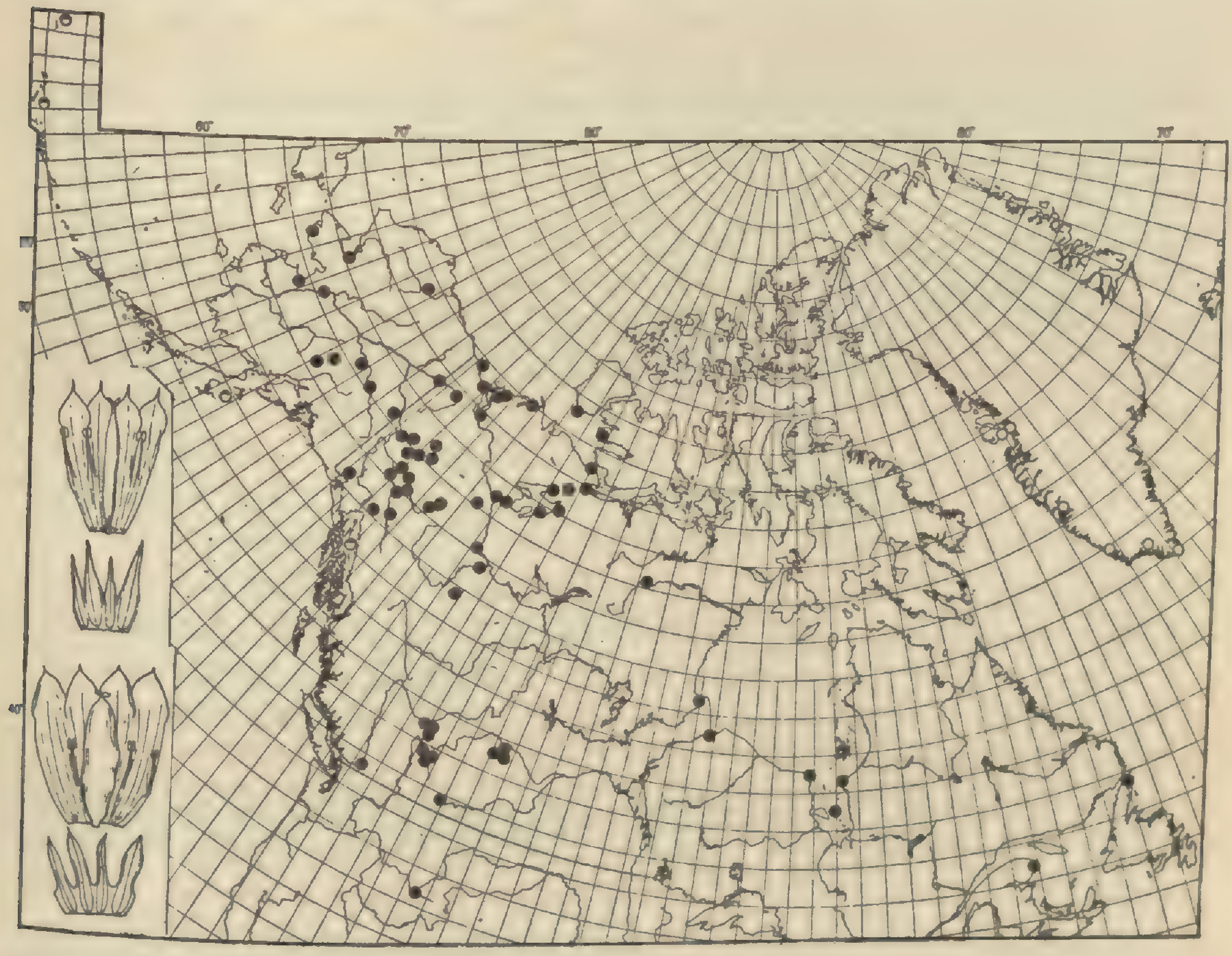
Gentiana aleutica Cham. & Schlecht. in Linnaea 1:175. 1826, ex char. (T.: *Chamisso & Eschscholtz s. n.*)

Gentiana unalaschcensis Cham. & Schlecht. loc. cit. 1826, nom. nud.

Throughout the Aleutian Islands, extending to the mainland as far as Juneau; mountains at elevations of 100–500 meters, in stony and mossy places, dry gullies and in grassy patches in gravel; flowering and fruiting throughout August.

UNITED STATES:

ALASKA: Mt. Roberts, Juneau, *Anderson 2139* (NY); Port Vita, Raspberry Island, Kodiak group, *Eyerdam 5236* (DAO); Semisopochnoi Island, *Coats 75* (US); Unimak Island, False Pass, *Eyerdam 2023* (NY, US); Jim Fishe Ridge, Attu Island, *Hardy 297* (MO); Attu Island, vicinity Massacre Bay, Lookout Hill, *Van Schaack 919* (MO), *935* (MO, US); Kodiak Island, Olga Bay, *Looff & Looff 543* (GH), *530* (UBC); valley near Cannery Station, *Looff & Looff 1689* (MO, NY); Volcano Mt., *Looff & Looff 1598* (CAN); Cold Bay, *Schofield 238* (DAO).



A B

Fig. 4. A, calyx and corolla of *Gentianella propinqua* (above), × ¾; and of *G. aurea* (below), × 1½. B, distribution of *G. propinqua* ssp. *propinqua* (black dots), of *G. propinqua* ssp. *aleutica* (half-black dots), and of *G. aurea* (circles).

7. GENTIANELLA AUREA (L.) H. Sm. ex Hylander, in Uppsala Univ. Arssk. 259. 1945.

Gentiana aurea L. Syst. ed. 10. 951, 1759. (T.: *Konig s. n.*, photo A!)
Gentiana quinquefolia Oeder, Fl. Dan. *t. 344.* 1766, not L., ex ic.
Gentiana involucrata Rottb. in Kiob. Skr. Selsk. 10:434. 1770. (T.: *Collector unknown*, C!)
Gentiana umbellata Marsch. & Bieb. Fl. Taur. Cauc. 3:188. 1819, ex char.
Gentiana aurea α borealis a. genuina Herder, in Acta Hort. Petrop. 1:438. 1872. (based on *G. aurea* L.)
Gentiana Pseud-Amarella Stev. ex Herder, loc. cit. 437. 1872, nom nud. in syn.

Annuals 2–30 cm. tall, simple or branched from the base, the branches curved-ascending, frequently bearing reduced flowers. Basal leaves frequently forming a rosette, elliptic to spatulate, the apex rounded to obtuse, attenuate to the base or to a slender petiole one-third the length of the blade, 3–21 mm. long, 1–10 mm. wide; median leaves lanceolate to ovate, the apex obtuse, the base rounded, 9–26 mm. long, 4–13 mm. wide; upper leaves similar and enclosing the terminal inflorescence. Flowers axillary, in simple or aggregate cymes or in dense terminal clusters, or rarely solitary, sessile or with short pedicels 1–13 mm. long, the lateral flowers sessile or with pedicels shorter than those of the terminal ones. Calyx 3–8 mm. long, generally 5-lobed, the tube 1.5–2.0 mm. long, the lobes linear to obovate, acute, two usually larger than the others, about two to three times as long as the tube, the margins ciliate to entire; sinuses rounded. Corolla blue to violet (?), tubular to narrowly funnelform, 6–11 mm. long, 3–5 mm. wide at the orifice; corolla lobes ovate, one-third the length of the tube, the tips mucronate, the sinuses acute, the orifice of the tube naked; interstaminal glands indistinct, scutiform, about 0.25 mm. above the base of the tube. Stamens included, the filaments inserted in the lower third of the corolla tube, the wings 0.25 mm. wide at the base and tapering above; anthers oblong, about 0.75 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil very shortly stipitate, the gynophore 0.5 mm. long, the ovary short-cylindrical to ovoid, about 6 mm. long, 1–2 mm. wide; stigmas sessile, about 0.25 mm. long and wide, oval and revolute. Capsules as long as the marcescent corollas or slightly longer. Seeds ovoid, slightly flattened, about 0.75 mm. long, 0.6 mm. wide, the surface smooth, minutely wrinkled under magnification, light brown.

In North America only in Greenland, but generally circumpolar, occurring in Norway and northern Russia, extending into the high mountains of southern Europe, the Caucasus, the Himalayan Mountains and in the province of Kansu, China; in Greenland growing in grassy fields at altitudes probably from sea-level to about 300 meters; in the Eurasian mountains at altitudes to 3200 meters; flowering from mid-July until mid-August; fruiting until early September (Greenland).

GREENLAND: Igdlungujak, *Jessen s. n.* (C); Tigsaluk, ca. 61° 21′, *Hartz s. n.* (C); Kingua, Tasersuak, *Hartz s. n.* (C); Tasermint, *Hartz s. n.* (C, GH, MO); Igaliko, *Hartz s. n.* (C); Kakasuak near Kringorsuak, *Kruuse s. n.* (C); Ekaluit i Igalikofjord, *Lindemann s. n.* (C); Frederiksdal, *Lundbolm s. n.* (C); Igaliko, *Meldorf s. n.* (C); Kagsiarsuk, Tunugdliarfik Fjord, *Petersen in 1880* (C); Tunugdliarfik Fjord, Qagsiarssuk, 61° 10′ N, 95° 30′ W., *Porsild 8897* (CAN); Kagsiarsuk, Igalikofjord, *Rosenvinge in 1888* (CAN);

Igaliko (Gardar), 60° 59′ N., *Porsild & Porsild s. n.* (C, GH); Igdlorssuit, Prins Christians Sund, 60° 10′ N., *Porsild & Porsild* (C); Igaliko, *Rosenvinge s. n.* (C); Kingua i Tunugdliarfik, *Rosenvinge s. n.* (C); Isarok v. Semdlik, *Rosenvinge s. n.* (C); Igaliko, *Sorenson s. n.* (C); Kakortok, *Vahl s. n.* (C); Igaliko, Dist. Julianehaab, *Vahl s. n.* (C).

Gentianella aurea is easily distinguished by the dense, terminal flower clusters subtended by the ovate upper leaves. Because of the characteristic curved-ascending basal branching pattern, *G. aurea* somewhat resembles *G. propinqua.* Although some depauperate specimens lack this feature, the mucronate corolla tips are a good supplementary character for recognition.

Very little material has been seen from Greenland, and therefore European specimens have been employed in drawing up the description, for the latter appear to be similar to the Greenland plants in every respect. Very little habitat data are given with the Greenland plants, so that this information also is drawn chiefly from the European collections.

8. Gentianella quinquefolia (L.) Small, Fl. Southeast. U. S. 929. 1903. (*G. quinquefolia* (L.) D. Löve in Hereditas 39:227. 1953, superfluous comb.).

Gentiana quinquefolia L. Sp. Pl. 1:230. 1753. (T.: *Kalm s. n.*, Sav. Cat. 328.31, photo A!)

Annuals (or biennials?) 2–8 dm. tall, profusely branched above, the branches curved-ascending, occasionally with the lower slender branches bearing reduced flowers, rarely simple in smaller plants. Basal leaves elliptic-spatulate to suborbicular, 10–22 mm. long, 4–10 mm. wide, the apex rounded, attenuate below to a slender petiole as long as the blade, soon withering and both basal and lower leaves usually deciduous; median leaves broadly ovate, acute, the base cordate to rounded, clasping, 15–60 mm. long, 5–35 mm. wide; upper leaves similar but progressively smaller. Flowers in compact, umbelliform, aggregate cymes, terminal on the branches, very rarely axillary and solitary; pedicels 2–17 mm. long, those of the subterminal node frequently longer than those of the terminal node. Calyx 4–10 mm. long, the tube 1.5–3.5 mm. long, the lobes about equal to or longer than the tube, triangular to elliptic-lanceolate, the margins entire, the sinuses acute to rounded. Corolla blue to white, narrowly funnelform, 15–20 mm. long, 4–7 mm. wide at the orifice; lobes ovate, half the length of the tube, the tips apiculate, the sinuses acute, the orifice of the tube naked; interstaminal glands scutiform, at the very base of the tube. Stamens included, the filaments inserted about the middle of the corolla tube, the wings strongly incurved, about 1 mm. wide at the base, tapering above; anthers oblong, 1.75 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil stipitate, the gynophore 2–3 mm. long; ovary cylindrical, 12 mm. long, 1.5 mm. wide; stigmas sessile, or with an indistinct style tapering into the ovary, oblong, 1 mm. long, 0.25 mm. wide, recurving. Capsule as long as the marcescent corolla, dehiscing at the tip. Seeds rounded or slightly flattened, 0.5–0.6 mm. long, the surface smooth, light brown.

A polymorphic species with two clearly distinct allopatric subspecies distinguished chiefly by flower and calyx size.

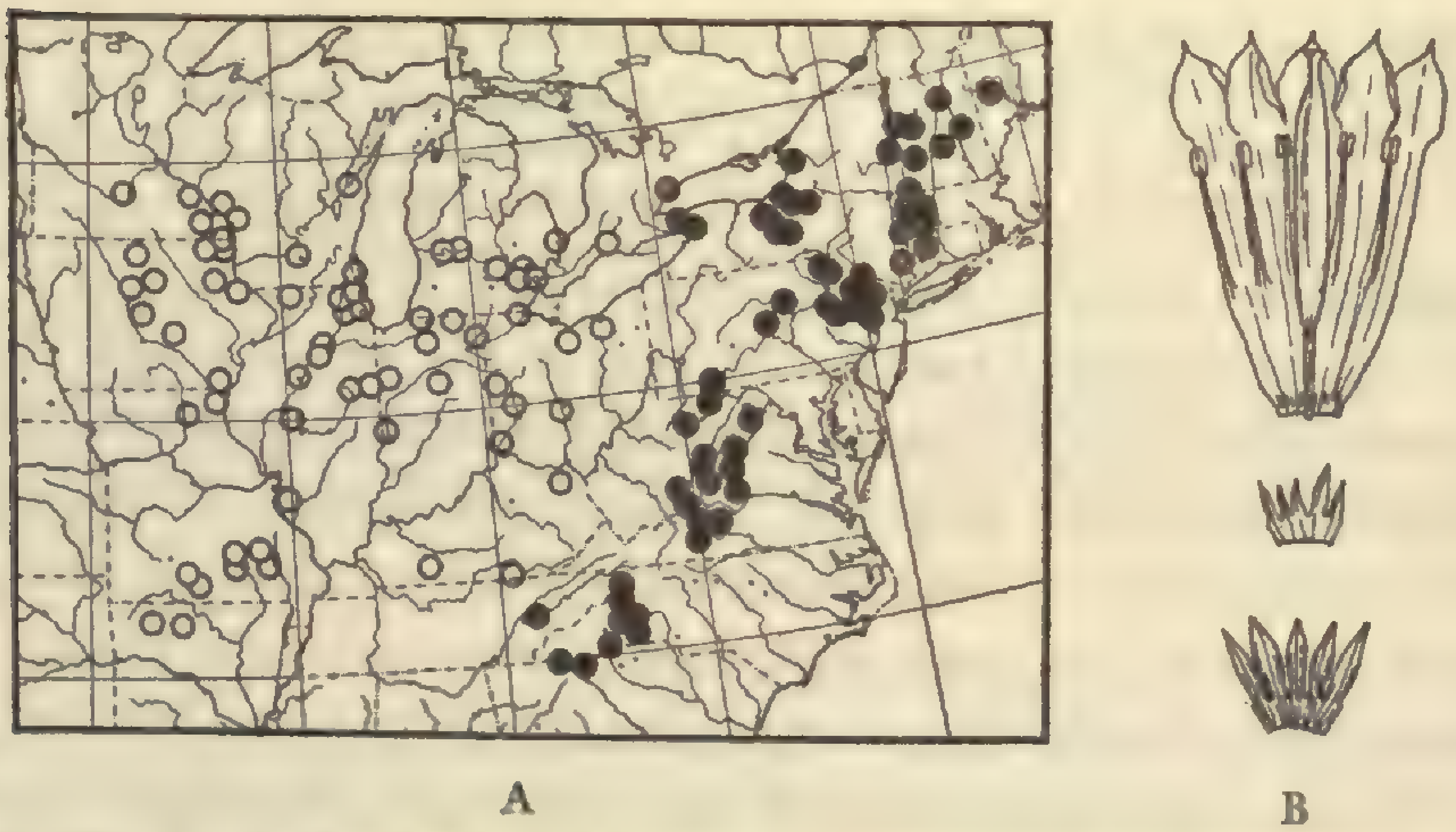


Fig. 5. A, distribution of *Gentianella quinquefolia* ssp. *quinquefolia* (black dots) and of ssp. *occidentalis* (circles). B, corolla of *G. quinquefolia* (top), calyx of ssp. *quinquefolia* (middle), and of ssp. *occidentalis* (bottom), × 1½.

KEY TO THE SUBSPECIES

a. Calyx 4–5 mm. long, the tube 1.5–2.0 mm. long, the lobes 2.0–2.5 mm. long, narrowly triangular with hyaline margins and very prominent keels; corolla 16–18 mm. long. Maine westward to New York and southern Ontario, southward to Georgia..8a. *G. quinquefolia* ssp. *quinquefolia*

aa. Calyx 8–10 mm. long, the tube 3.0–3.5 mm. long, the lobes 5–6 mm. long, elliptic-lanceolate to oblanceolate with thickened margins and broadly flattened, frequently nerve-like, keels; corolla about 20 mm. long. Ohio to Minnesota, southward to Arkansas and Kentucky..8b. *G. quinquefolia* ssp. *occidentalis*

8a. Gentianella quinquefolia (L.) Small, ssp. quinquefolia

Gentiana quinqueflora Lam. Encyc. 2. 643. 1768, sphalm?
Hippion quinquefolium (L.) Schmidt, in Roem. Archiv f. Bot. 1:11. 1796.
Gentiana amarelloides Michx. Fl. Bor. Am. 1:175. 1805. (T.: *Michaux s. n.*, photo MO!)
Aloitis parviflora Raf. Fl. Tellur. 3:21. 1837, ex char.
Aloitis quinqueflora (L. emend. Lam.) Raf. loc. cit. 22. 1837.
Gentiana quinqueflora Lam. β *parviflora* Raf. ex Griseb. in DC. Prod. 9:100. 1845, ex char.
Gentiana quinquefolia L. var. *amarelloides* (Michx.) Britt. in Mem. Torr. Bot. Club 5:260. 1894.
Aloitis divaricata Greene, Leafl. Bot. Obs. & Crit. 1:94. 1904.
Amarella amarelloides (Michx.) Greene, loc. cit. 53. 1904.
Gentiana quinquefolia L. f. *lutescens* Fern. in Rhodora 19:151. 1917. (T.: *Porter s. n.*!)

Maine to New York and southern Ontario southward in the Appalachians to North Carolina and Tennessee, at altitudes up to 1800 meters in the southern Appalachians; in a variety of habitats, but chiefly on edges of woods in shady places, roadsides, and along stream banks; apparently preferring limestone areas or lime soils; flowering from early September until early October, rarely until November; fruiting during the latter part of October.

Canada:

ontario: Elgin Co.: *Fisher s. n.* (MO). Lambton Co.: Forest, *Dodge s. n.* (MO). Welland Co.: Niagara Falls, *Scott s. n.* (US). York Co.: Toronto, *Armstrong s. n.* (US).

UNITED STATES:

CONNECTICUT: Litchfield Co.: South Canaan, *Greenman 1444* (GH, MO).

GEORGIA: Rabun Co.: Blalock, *Wherry & Pennell 14087* (F, MO).

MAINE: Oxford Co.: Norway, *Olmstead s. n.* (GH).

MARYLAND: Garrett Co.: Oakland, *Hermann 11380* (MO).

MASSACHUSETTS: Berkshire Co.: Kitchen Brook, *Churchill s. n.* (GH, MO).

NEW HAMPSHIRE: Grafton Co.: Squam Lake, *Faxon s. n.* (GH, US).

NEW JERSEY: Sussex Co.: High Point, *Mackenzie 4408* (MO). Warren Co.: Phillipsburg, *Garber s. n.* (WS).

NEW YORK: Cayuga Co.: *Hall s. n.* (MO). Columbia Co.: Columbiaville, *McVaugh 4037* (GH). Dutchess Co.: Clove, *Standley & Bollman 12361* (US). Erie Co.: *Clinton s. n.* (NY). Jefferson Co.: Watertown, *Keyes s. n.* (US). Madison Co.: Chittenango, *Morong s. n.* (US). Onondaga Co.: Syracuse, *Overacker s. n.* (MO). Orange Co.: Brookfield, *Collector unknown* (MO). Oswego Co.: Phoenix, *Hastings s. n.* (NY). Schuyler Co.: Hector, *Wright 10612* (GH). Seneca Co.: West Junius, *Schrenk s. n.* (MO). Tompkins Co.: Ithaca, *Sheldon s. n.* (US). Warren Co.: Lake George, *House 25991* (MO). Washington Co.: Tripoli, *Burnham s. n.* (GH).

NORTH CAROLINA: Buncombe Co.: Biltmore, *Biltmore Herb. 465b* (GH, MO, US). Haywood Co.: Pisgah Forest, *House 3696* (GH). McDowell Co.: Little Roan, *Merriam s. n.* (GH, MO, NY, US). Polk Co.: Columbus, *Townsend s. n.* (US). Yancey Co.: Busick, *Wherry & Pennell 14279* (MO).

PENNSYLVANIA: Center Co.: Coburn, *Whyl 271* (GH). Chester Co.: *Porter s. n.* (GH). Lackawanna Co.: Carbondale, *Topping s. n.* (US). Luzerne Co.: Long Pond, *Small & Heller s. n.* (US). Lycoming Co.: Williamsport, *Smith s. n.* (PH). Monroe Co.: Naomi Pines, *Small s. n.* (US). Northhampton Co.: Easton, *Heller 630* (MO, US). Somerset Co.: *Rothrock s. n.* (F).

TENNESSEE: Carter Co.: Roan Mountain, *Britton & Britton s. n.* (NY).

VERMONT: Addison Co.: Weybridge, *Brainerd s. n.* (NY). Bennington Co.: Manchester, *Day 405* (US). Caledonia Co.: East Barnett, *Blanchard s. n.* (GH). Orange Co.: Strafford, *Jones s. n.* (GH); Rutland, *Eggleston 1503* (US).

VIRGINIA: Augusta Co.: Augusta Springs, *Steele s. n.* (MO, US)) Bedford Co.: Peaks of Otter, *Beyrich 87* (MO, NY). Botetourt Co.: Apple Orchard Mountain, *Freer 1902* (GH). Frederick Co.: Cedar Creek, *Canby s. n.* (US). Highland Co.: Shenandoah Mt., *Rawlinson 272* (US). Madison Co.: Shenandoah Nat. Park, *Graf 3* (US). Nelson Co.: Afton, *Steele s. n.* (US). Page Co.: Hawksbill Mt., *Baldwin 5461* (GH). Roanoke Co.: Singer, *Wood 5701* (GH). Rockbridge Co.: *Steele s. n.* (US).

WEST VIRGINIA: Greenbrier Co.: Kate's Mt., *Hunnewell 7105* (GH). Monroe and Allegheny Cos.: Allegheny Station, *Steele & Steele 418* (GH, MO, US). Pendleton Co.: Lake Terra Alta, *Berkley 1781* (MO). Preston Co.: Brookside, *Olds s. n.* (US).

8b. GENTIANELLA QUINQUEFOLIA (L.) Small, ssp. **occidentalis** (A. Gray) J. M. Gillett, comb. & stat. nov.

Gentiana quinqueflora Lam. var. *occidentalis* A. Gray, Man. ed. 1, 359. 1848, based on Hook. Bot. Mag. 63: *t. 3496.* 1836. (c.f. Gray in Syn. Fl. N. Amer. 2:119. 1878).

Gentiana quinquefolia L. var. *occidentalis* (A. Gray) A. S. Hitchc. in Trans. Acad. Sci. St. Louis 5:508. 1891.

Gentianella quinquefolia (L.) Small, var. *occidentalis* (A. Gray) Small, Fl. Southeast. U.S. 929. 1903.

Amarella occidentalis (A. Gray) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Aloitis mesochora Greene, loc. cit. 94. 1904, ex char.

Aloitis occidentalis (A. Gray) Greene, loc. cit. 1904.

Aloitis foliosa Greene, loc. cit. 1904. (T.: *Moseley s. n.!*)

Gentiana occidentalis (A. Gray) Fitzpat. in Iowa Nat. 2:13. 1906.

Ohio westward to Wisconsin, Iowa and Minnesota, south to Arkansas and Kentucky; occurring in much the same habitats as the typical subspecies but also found on prairies and along wooded oak-juniper bluffs and wooded hillsides; as in the

typical subspecies, seeming to prefer limestone areas and wet stream gullies; flowering dates similar to the typical subspecies.

United States:

arkansas: Newton Co.: Vendor, *Iltis s. n.* (U. Ark.). Stone Co.: Blanchard Springs, *Iltis s. n.* (U. Ark.).

illinois: Champaign Co.: Rantoul, *Gleason s. n.* (GH). Cook Co.: Glencoe, *Umbach s. n.* (GH, PH). Hancock Co.: Augusta, *Mead s. n.* (MO). Lake Co.: Lake Forest, *Jensen 113* (MO). Kane Co.: Aurora, *Kane s. n.* (PH, US). LaSalle Co.: Ottawa, *Huett s. n.* (GH). Menard Co.: Athens, *Hall s. n.* (MO, PH, US). Peoria Co.: Peoria, *McDonald s. n.* (GH, NY). St. Clair Co.: French Village, *Eggert s. n.* (GH, MO). Stephenson Co.: Freeport, *Johnson s. n.* (US). Tazewell Co.: East Peoria, *Chase 3724* (US). Vermilion Co.: Fithian, *Gates 2175* (US).

indiana: Allen Co.: St. Joe River, Robinson Park, *Deam 606* (MO, NY, US). Benton Co.: *Shipman s. n.* (PH). Howard Co.: Wildcat, *Collector unknown* (NY). Lagrange Co.: Mongo, *Deam 19264* (GH). Marshall Co.: Lake Maxinkuckee, *Scovell & Clark 1459* (US). St. Joseph Co.: Notre Dame, *Nieuwland 10406* (US). Vigo Co.: Terre Haute, *Evermann s. n.* (US).

iowa: Allamakee Co.: Hanover Twp., *Tolstead s. n.* (MO). Cerro Gordo Co.: Mason City, *Shimek s. n.* (WS). Dubuque Co.: Luxemburg, *Shimek s. n.* (MO). Fayette Co.: *Fink 487* (GH, US). Hamilton Co.: Webster City, *Hayden 10221* (GH). Hardin Co.: Iowa Falls, *Peck s. n.* (GH). Poweshiek Co.: Grinnell, *Jones s. n.* (GH). Story Co.: Ames, *Bessey 301* (GH, MO, US). Van Buren Co.: Bentonsport, *Graves s. n.* (MO). Winneshiek Co.: Ridgeway, *Hayden 10222* (US).

kentucky: *Short s. n.* (MO, PH).

michigan: Genesee Co.: Flint, *Clark 5* (US). Ingham Co.: Lansing, *Tracy s. n.* (US). Ionia Co.: Hubbardston, *Wheeler s. n.* (US). Kent Co.: Grand Rapids, *Cole s. n.* (MO). Saint Clair Co.: Port Huron, *Dodge s. n.* (GH, MO). Washtenaw Co.: Dexter, *Palmer s. n.* (US). Wayne Co.: Woodbridge Park, *Chandler s. n.* (US).

minnesota: Houston Co.: *Freiberg s. n.* (MO). Nicollet Co.: St. Peters, *Geyer 234* (MO). Olmstead Co.: Pleasant Grove Twp., *Moore, Leedy & Thatcher 15689* (DAO). Wabasha Co.: Lake City, *Manning s. n.* (GH). Winona Co.: Whitman, *Moore & Neva 16152* (MO, WS).

missouri: Adair Co.: *Broadhead s. n.* (MO). Carter Co.: Van Buren, *Palmer 19450* (MO). Clark Co.: *Bush s. n.* (MO, NY). Douglas Co.: Hebron, *Steyermark 65102* (F). Howell Co.: 5 mi. s.w. Willow Springs, *Steyermark 66795* (DAO, F). Franklin Co.: Pacific, *Eggert s. n.* (MO). Iron Co.: Royal Gorge, *Kellogg 15260* (MO). Madison Co.: Jewett, *Steyermark 20985* (MO). Reynolds Co.: Lesterville, *Steyermark 20885* (MO). Shannon Co.: Monteer, *Steyermark 8771* (MO).

ohio: Cuhahoga Co.: *Cook s. n.* (GH). Erie Co.: East Fork, Vermilion River, *Moseley s. n.* (F, MO, US). Franklin Co.: Georgeville, *Werner 539* (GH). Hamilton Co.: *Collector unknown* (PH). Lucas Co.: Monclova, *Moseley s. n.* (F, US). Mercer Co.: *Collector unknown* (PH). Montgomery Co.: Dayton, *Short s. n.* (PH).

wisconsin: Brown Co.: Scott, *Schuette s. n.* (GH). Buffalo Co.: Fountain City, *Palmer 28496* (MO). Dane Co. Madison, *McMurphy s. n.* (US). Lacrosse Co.: *Pammel s. n.* (MO). Racine and Kenosha Cos.: *Wadmond s. n.* (PH). Vernon Co.: Coon Valley, *Marks 1988* (DAO).

9. Gentianella **microcalyx** (Lemmon) J. M. Gillett, comb. nov.

Gentiana microcalyx Lemmon in Pacific Rural Press 23:129. Feb. 25, 1882; Engelm. ex A. Gray, in Proc. Amer. Acad. 17:222. 1882. (T.: *Lemmon 584*!)
Amarella microcalyx (Lemmon) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Annuals 15–45 cm. tall; stems prominently angled, generally branched above, rarely from the base, the branches sharply ascending. Basal leaves oblanceolate, elliptic, to spatulate, the apex rounded to obtuse, attenuate to the base, 10–25 mm.

long, 2–8 mm. wide, soon withering and deciduous; median leaves broadly ovate to lanceolate-ovate, the apex acute, cordate or rounded and clasping at the base, 5–40 mm. long, 3–20 mm. wide; upper leaves similar to the median, becoming progressively more lanceolate. Flowers perfect, occasionally unisexual by abortion of the anthers (or, more rarely, the pistil), in compact umbelliform aggregate cymes, terminal on the branches, very rarely axillary and solitary; pedicels of the terminal flowers about equal, 3–15 mm. long. Calyx minute, 2.0–2.5 mm. long, 4- to 5-lobed, the tube 1 mm. long; lobes triangular, acute, essentially regular, about equal to the length of the tube or slightly longer, the margins entire, the sinuses rounded. Corolla white to pale lavender, tubular, narrowly funnelform or salverform when the lobes are fully expanded, about 10 mm. long, 2–3 mm. wide at the orifice; lobes oblong, one-third to half as long as the tube, the tips obtuse to rounded, the sinuses acute, the orifice of the tube naked; interstaminal glands indistinct, appearing only as dark oblong stains by transmitted light, 0.5 mm. from the base of the tube. Stamens slightly exserted; filaments inserted near the upper third of the corolla tube, scarcely winged, the wings about 0.25 mm. wide at the base, tapering above; anthers oblong, 1.3 mm. long, 0.8 mm. wide, versatile and attached near the middle. Pistil shortly stipitate, the gynophore 0.5 mm. long, ovary cylindrical, 11 mm. long, about 2 mm. wide; stigmas sessile, oblong, 0.4 mm. long, 0.2 mm. wide, erect. Mature capsule longer than the marcescent corolla, 12 mm. long, dehiscing at the tip. Seeds ovoid, slightly flattened, 0.75 mm. long, 0.5 mm. wide, smooth, light brown.

In the Huachuca Mountains of Cochise County, the Rincon and Santa Catalina mountains of Pima County, and in the Santa Rita Mountains of both Pima and Santa Cruz counties, Arizona; in Mexico in the Sierra Madres of southwestern and central Chihuahua, eastern Sonora, eastwards in the mountains about Cuatro Cienagas, Coahuila, southward to Durango; in cool moist pine-oak forest and on burnt-over slopes at altitudes of 600–2000 meters; flowering from late August until the end of September; fruiting in October.

United States:

arizona: Cochise Co.: Huachuca Mts., Carr Peak, *Goodding 858* (GH, NY); Carr Canyon, *Gould & Haskell 3373* (GH, MO), *Jones s. n.* (GH); Ramsey Canyon, *Jones 24967* (GH, MO, NY), *Lemmon 584* (GH, MO, US); Cave Canyon, *Lemmon 2822* (F, GH, US), *Peebles, Harrison et al. 3399* (US); Fort Huachuca, *Wilcox 507* (US); Towner's Canyon, *Wilcox s. n.* (NY). Pima Co.: Rincon Mts., Manning Camp, *Blumer s. n.* (F, GH, MO); Santa Rita Mts., *Griffiths 6049* (US), *Griffiths & Thornber 182* (US), *Loomis 3269* (US); Santa Catalina Mts., Mt. Lemmon, *Harrison 3020* (US), *Heally 191* (US); Marshall Gulch, *Shreve 5394* (GH, UC, US). Santa Cruz Co.: Santa Rita Mts., Kent Canyon, *Pilsbry s. n.* (PH), *Wooton s. n.* (US); location unknown, *Toumey s. n.* (US).

Mexico:

chihuahua: Temosachic, Madera, *Muller 3465* (GH).

coahuila: Cuatro Cienagas, Sierra de la Madera, *Muller 3235* (MO).

durango: Barranca Sandia Station, *Pringle 13660* (GH).

sonora: Rio de Bavispe, 4 mi. e. El Belito, *White 4771* (GH).

Series II. **AMARELLAE** J. M. Gillett, ser. nov.

Amarella Gilib. Fl. Lith. Inch. 1:36. 1781, nom nud.; Raf. Fl. Tellur. 3:20. 1837. (T.: *Anthopogon amarella* (L.) Raf.)
Gentiana L. *Coelanthae Froel. Gent. Diss. 15. 1796, proparte.
Gentiana L. ****Endotrichae* Froel. loc. cit. 86. 1796, ut sectio Murbeck, in Acta Hort. Berg. 23:1–28. 1892.
Eyrythalia Borckh. in Roem. Archiv f. Bot. 1:28. 1796, pro parte maj.
Gentiana L. ***Amarella* Gaudin, Fl. Helv. 2:270. 1828; ut sectio Griseb. Gen. et Sp. Gent. 238. 1839.

10. Gentianella **tortuosa** (M. E. Jones) J. M. Gillett, comb. nov.

Gentiana tortuosa M. E. Jones, in Proc. Calif. Acad. II, 5:707. 1895. (T.: *M. E. Jones 6008*!)
Amarella tortuosa (M. E. Jones) Rydb. in Bull. Torr. Bot. Club 40:463. 1913.
Gentiana helleri Briq. in Candollea 4:331. 1931. (T.: *Heller 11072*!)

Acaulescent or caulescent, cespitose annuals 2–8 cm. tall, from very long taproots. Basal leaves elliptic, lingulate, to spatulate, the apex rounded or obtuse, attenuate below to about the width of the stem, clasping, 5–25 mm. long, 2–6 mm. wide; median leaves elliptic, oblong, or lanceolate, obtuse to acute, the base attenuate, 5–35 mm. long, 1–5 mm. wide. Flowers solitary in the axils of the stem leaves, or on short axillary branches; pedicels short to 15 mm. long. Calyx 5–7 mm. long, the tube very short, 1–2 mm. long, the lobes closely enclosing the corolla tube, linear to oblanceolate, acute, unequal, the margin hyaline and papillose, the sinuses rounded. Corolla white (or pale blue?), broadly funnelform to somewhat campanulate, 5–8 mm. long, 3–4 mm. wide; lobes ovate, obtuse, equaling the length of the tube, bearing a corona of 2–10 hyaline, papillose-margined fimbriae one-third the length of the lobes and extending across the base or in two distinct clusters on each side, the lower flowers occasionally naked, the sinuses acute; inter-staminal glands rather indistinct, appearing as pale green scutiform patches at the very base of the corolla tube. Stamens included, the filaments inserted in the lower half or third of the tube, the wings 0.25 wide at the base; anthers short, oblong, 0.8 mm. long, 0.6 mm. wide, versatile. Pistil short-stipitate, the gynophore 0.3–0.5 mm. long; ovary elliptic-ovoid, 4–5 mm. long; stigmas sessile, elliptic, 0.5 mm. long, 0.3 mm. wide, erect. Mature capsule as long as the marcescent corolla or slightly exserted, dehiscing in the upper half. Seeds elongate-ovoid, about 1.2 mm. long, 0.7 mm. wide, very slightly flattened, minutely wrinkled under magnification, light brown.

Mountains of southwestern Utah and southern Nevada; along damp banks and on open hillsides and bare gravelly slopes among yellow pine at elevations of 2600–3300 meters; flowering from mid-July until late August; fruiting in September.

United States:

nevada: Clark Co.: Ridge to Charleston Peak, *Clokey 7625* (GH, MO, NY, US, WS); Rainbow Falls, *Clokey 8061* (NY); head of Lee Canyon, Charleston Mts., *Heller 11072* (GH, MO, NY, US).

utah: Garfield Co.: Bryce Canyon, *Eastwood & Howell 7230* (US); Panguitch Lake, *M. E. Jones 6008* (US). Iron Co.: Cedar Breaks, *Hitchcock, Rathke, & Van Raadshooven 4586* (UC, WS). Kane Co.: 27 mi. s. Panguitch, *Maguire 19646* (WS).

Fig. 6. Distribution of *Gentianella tortuosa* in Utah and Nevada.

Gentianella tortuosa, a very distinct species, appears to be rather localized since the collections came from only five localities. Distinctive field characters include the cespitose habit and the very numerous, somewhat campanulate flowers borne throughout the plant. The very long slender tap-root, sometimes twice as long as the aerial part of the plant, is a feature unique in this species.

The key appears to indicate a close alliance of *G. tortuosa* and *G. amarella* ssp. *acuta.* It would be unwise, however, to venture an opinion on relationships here, since the floral morphology, exclusive of size differences, is startlingly similar in many species of section AMARELLA, while in vegetative characters the plants are quite different. In floral morphology, *G. tortuosa* bears a great similarity to *G. aurea* of Greenland, except for the obvious expansion of the corolla itself and the presence of fimbriae in the throat. Since in so many instances in other species the presence or absence of fimbriae in the corolla orifice has proved to be an unreliable character, the presence of fimbriae should not be considered discordant. The ovoid ovary is a more reliable character to suggest affinity with *G. aurea,* since all other species within the section have distinctly cylindrical ovaries which are almost indistinguishable from one another except for size. Considering purely vegetative characters, the branching pattern of *G. tortuosa,* consisting as it does of many stems, suggests affinity with *G. amarella* ssp. *acuta.* The few fimbriae in *G. tortuosa* are hyaline and short, but although frequently found in two phalanges or groups on either side of the midvein, possess distinct vascular bundles.

11. GENTIANELLA AMARELLA (L.) Börner, Fl. deut. Volk, 543. 1912. (H. Smith in Hylander, in Uppsala Univ. Arssk. 259. 1945, superfluous comb.)

Gentiana amarella L. Sp. Pl. ed. 1, 230. 1753. (T.: *Linn. Herb. 328.32,* photo, A!)[59]

Annuals 5–70 cm. tall, simple or branched from the base or above, the basal branches occasionally bearing reduced flowers, the upper cauline branches frequently reduced. Basal leaves elliptic, lingulate to spatulate, the apex obtuse to

[59] Eurasian synonyms other than the basonym are not included here.

rounded, attenuate to the base or to a slender petiole as long as or shorter than the blade, frequently forming basal rosettes or soon withering, 3–40 mm. long, 1–11 mm. wide; median leaves oblanceolate, elliptic, ovate to ovate-lanceolate, the apex acute, occasionally obtuse or rounded in western forms, the base rounded to cordate, subconnate to somewhat decurrent or clasping, 8–60 mm. long, 3–20 mm. wide; upper leaves similar to the median or becoming progressively smaller and more acute. Flowers few to very numerous, axillary or terminal, in simple or aggregate cymes, frequently in dense clusters or solitary in the axils, sessile or borne on pedicels up to 5 cm. long. Calyx 5–25 mm. long, 4- to 5-lobed, the tube 2–40 mm. long, the lobes various, regular to irregular, one or more slightly larger than the remainder or becoming foliaceous, the margins entire, minutely denticulate to ciliate, the sinuses acute to somewhat rounded. Corolla white, blue, mauve, or yellow, or with a greenish tube, tubular, narrowly funnelform to salverform when the lobes are fully expanded, 10–25 mm. long, 2–6 mm. wide at the orifice, the lobes ovate to ovate-oblong, half the length of the tube, the tips obtuse to acute, the sinuses acute, the base of each lobe bearing a few to many slender fimbriae, free or united at the base to form a fimbriate scale; interstaminal glands at the base of the tube, scutiform. Stamens included, the filaments inserted in the lower half of the corolla tube, the wings 0.5–0.75 mm. wide at the base, slightly tapering above; anthers oblong, 0.75–1.5 mm. long. Pistil sessile or shortly stipitate, the gynophore up to 0.5–1.0 mm. long; ovary cylindrical to cylindric-ovoid, about 8–15 mm. long, 1-4 mm. mide; stigmas sessile, elliptic to oblong, erect or recurved, 0.7–1.5 mm. long, 0.5–0.7 mm. wide. Capsule as long as the marcescent corolla or slightly exceeding it, dehiscing at the tip, the valves slightly spreading. Seeds variable, ovoid, slightly flattened, 0.5–1.0 mm. long, about 0.75–1.0 mm. wide, the surface smooth.

Throughout the northern temperate and arctic zones of Europe, Asia, and America, segregating into a large number of populations. In North America represented by five subspecies extending from the Arctic coasts and interior of Alaska to central Mexico; northeastward to Newfoundland and Maine, but not found in the greater Mississippi River basin nor in the eastern or southeastern United States.

The typical subspecies, *amarella*, occurs in central and western Europe and appears to be distinguished from ssp. *acuta* chiefly by its large flowers. Since ssp. *amarella* does not occur in North America, it is not described in this revision.

KEY TO THE SUBSPECIES

a. One or more calyx lobes broadly foliaceous and enveloping the others; corona fimbriae united below to form a scale; stem with few (3–5) internodes; seeds about 1 mm. in diameter. Eastern and southern Utah and adjacent states.........11a. *G. amarella* ssp. *heterosepala**

aa. Calyx lobes regular or irregular but never foliaceous; corona fimbriae free; stems with 5–12 or more internodes; seeds 0.75 mm. in diameter or less.

b. Lateral veins of the calyx lobes essentially parallel for some distance below the sinus, uniting towards the base of the tube. Highly variable subspecies with numerous local races. Newfoundland, Maine, and Vermont, westward to Alaska, southward in the western mountains to Baja California and central Mexico.................11b. *G. amarella* ssp. *acuta**

bb. Lateral veins of the calyx lobes uniting immediately below the sinus.
c. Calyx 5–11 mm. long, the tube 2–3 mm. long, the lobes thinly membranaceous.
d. Flowers in simple or aggregate cymes or axillary branches, 8–12 mm. long, mauve, with essentially erect corolla lobes. Southern and central Mexico..11c. *G. amarella* ssp. *mexicana*
dd. Flowers chiefly in terminal umbelliform aggregate cymes, 9–17 mm. long, white, with spreading purple-speckled corolla lobes. North-central Mexico..11d. *G. amarella* ssp. *sandiana*
cc. Calyx 12–15 mm. long, the tube 3–4 mm. long, the lobes somewhat coriaceous.
e. Flowers 20–25 mm. long, frequently borne in compact clusters in the axils of upper leaves; plants 25–70 cm. tall. Northern Mexico and adjacent New Mexico. ....11e. *G. amarella* ssp. *wrightii*
ee. Flowers 15–20 mm. long, in compact or loose clusters throughout the plant; plants 5–40 cm. tall. South-central Mexico in Michoacan and Mexico..11f. *G. amarella* ssp. *hartwegii*

* *G. amarella* ssp. *heterosepala* grades into ssp. *acuta* with numerous intermediate forms.

11a. Gentianella amarella (L.) Börner, ssp. **heterosepala** (Engelm.) J. M. Gillett, comb. & stat. nov.

Gentiana heterosepala Engelm. in Trans. Acad. Sci. St. Louis 2:215. 1862. (T.: *Engelmann s. n.*!)
Gentiana distegia Greene, Pittonia 4:182. 1900. (T.: *Baker s. n.*!)
Amarella heterosepala (Engelm.) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.
Amarella scopulorum Greene, loc. cit. 55. 1904, ex char.
Gentiana polyantha A. Nels. in Bot. Gaz. 56:68. 1913. (T.: *Walker 513*!)
Gentiana scopulorum (Greene) Tidestrom, in Contr. U.S. Nat. Herb. 25:415–416. 1925.

Most common in Utah and extending into Colorado, Wyoming, New Mexico, Arizona and Idaho; in moist meadows and open aspen forests, from 2600 to 3200 meters; flowering from mid-July through August; fruiting from late August until September.

United States:

Arizona: Apache Co.: Hannagan Meadow, White Mts., *Kearney & Peebles 12412* (US). Coconino Co.: Grand Canyon of the Colorado, *MacDougal 173a* (GH, US); San Francisco Mts., *Lemmon & Lemmon s. n.* (US).

Colorado: Boulder Co.: Ward to Nederland, *Weber 5734* (DAO). Delta Co.: Leroux Creek, *Cowen 92* (GH). Dolores Co.: *Ownbey 1478* (GH, MO, WS). Gunnison Co.: Gunnison Forest, *Eggleston 14631* (GH, US). Mineral Co.: near Pagosa Peak, *Baker s. n.* (ND), *Baker 518* (GH, MO, NY, US). Montrose Co.: Tabeguache Basin, *Payson 169* (GH, MO). San Miguel Co.: Iron Springs Mesa, *Walker 513* (GH, RM, WS).

Idaho: Nez Perce Co.: Zaza, *St. John & Muller 8634* (WS).

New Mexico: Grant Co.: Black Range, *Metcalf 1257* (GH, NY, US). Otero Co.: Sacramento Mts., *Wooton s. n.* (US). Rio Arriba Co.: Brazos Canyon, *Standley & Bellman 10654* (US). Sandoval Co.: Sandia Mts., *Ellis 225* (MO, NY, US). San Juan Co.: Tunitch Mts., *Standley 7716* (US).

Utah: Duchesne Co.: Cottonwood Canyon, *Watson 942* (GH). Emery Co.: Muddy Creek region, *Tidestrom 499* (US). Grand Co.: La Sal Mts., *Payson & Payson 4073* (GH, MO). Iron Co.: Cedar Breaks National Monument, *Gould 2051* (NY, US); Spring Lake, *Parry s. n.* (MO). Piute Co.: Tate Mine, Marysvale, *Jones s. n.* (US); Wasatch Mts., *Jones 1138* (GH, NY). San Juan Co.: La Sal Mts., *Purpus 7033* (MO, US). Sevier Co.: Fish Lake, *Jones 5723* (MO, US). Summit Co.: Uintah Mts., *Engelmann s. n.* (MO), *Payson & Payson 5067* (GH, MO, NY, US, WS). Utah Co.: Utah Lake, *Parry 61* (MO, NY, US). Wasatch Co.: Clayton Peak, Wasatch Mts., *Stokes s. n.* (MO, US). Wayne Co.: Thousand Lakes Mountain, Fish Lake Nat. Forest, *Johnson 81* (PH).

Wyoming: Big Horn Co.: *Worthley 59* (US). Lincoln Co.: Cottonwood Lake, e. of Smoot, *Payson & Armstrong 3765* (GH, MO).

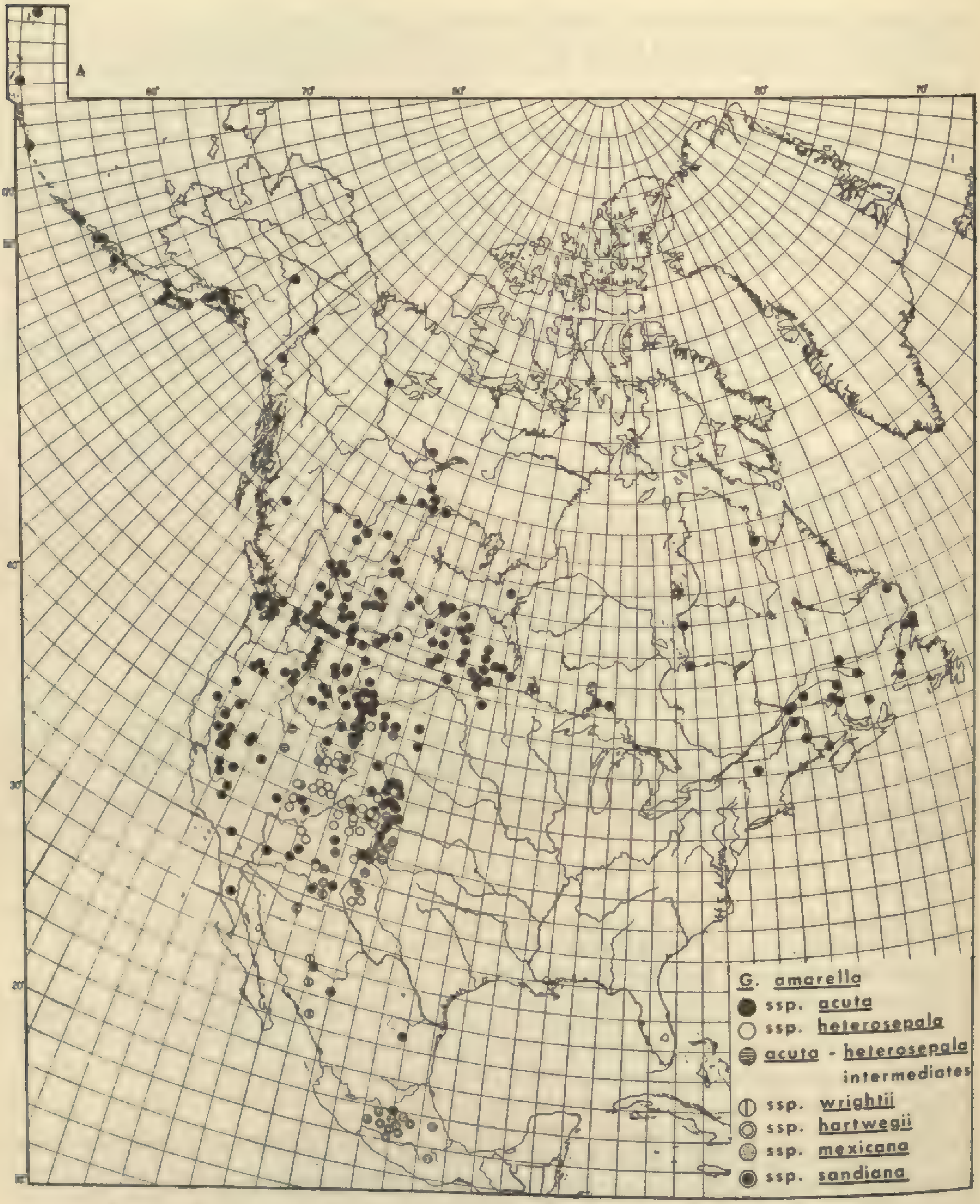


Fig. 7. Distribution of the subspecies of *Gentianella amarella* in North America.

Engelmann's *Gentiana heterosepala* is reduced to subspecific rank because neither the characters are sufficiently stable nor the range sufficiently isolated to warrant recognition as a species. A center of plants of somewhat pure ssp. *heterosepala* occurs in Utah, New Mexico, and Colorado. However, there are inumerable intergrades with ssp. *acuta* at the borders of its range. Plants of ssp. *acuta* throughout Wyoming and as far north as Montana show traces of *heterosepala* characters and various forms from this population have been described as species. Most of these I am placing in the synonomy of ssp. *acuta* since they lack the foliaceous calyx and many other characters of ssp. *heterosepala.* Undoubtedly this problem is too complex to solve completely by herbarium methods and it will be necessary to make further studies to define the groups properly.

The singular foliaceous calyx of ssp. *heterosepala* is paralleled in Europe by *G. campestris*. *Heterosepala* tendencies observed in this population include:

1. Tendency toward larger flowers.
2. Enlargement of one or more calyx lobes.
3. Fewer stem nodes.
4. Congestion of flowers by a shortening of lateral branches (var. *strictiflora* Rydb., a condition greatly affected by habitat conditions).
5. Larger, fewer seeds.
6. Thickening of the stem.
7. Larger cauline leaves accompanied by a trend from acute to obtuse leaves.
8. Fusion of faucal fimbriae.
9. Congestion of the upper nodes
10. Trend from triangular to oblong calyx lobes.

Shortening of upper internodes is a trend found also in *G. propinqua* and in *G. aurea.*

11b. Gentianella amarella (L.) Börner, ssp. **acuta** (Michx.) J. M. Gillett, comb. & stat. nov.

Gentiana acuta Michx. Fl. Bor. Amer. 1:177. 1803. (T.: *Michaux s. n.* photo MO!)
Gentiana axillaris Raf. Med. Fl. 1:213. 1828, ex char.
Gentiana plebeja Cham. ex Bunge, in Mem. Soc. Nat. Mosc. 7 (Nouv. Mem. Soc. Nat. Mosc. 1): 250. *t. 29. f. 5.* 1829, ex ic.
Amarella acuta (Michx.) Raf. Fl. Tellur. 3:21. 1837.
Ericala acuta (Michx.) G. Don, Gen. Syst. 4:190. 1838.
Gentiana acuta Michx. *β stricta* Griseb. Gen. & Sp. Gent. 242. 1839. (T.: *Drummond* s. n., photo MO!)
Gentiana tenuis Griseb. loc. cit. 250. 1839. (T.: *Richardson s. n.*, photo MO!)
Gentiana aggregata Bunge, ex Griseb. in DC. Prod. 9:100. 1845, nom. nud. in syn.
Gentiana acuta Michx. var. *nana* Engelm. in Trans. Acad. Sci. St. Louis 2:214. 1862. (T.: *Parry 309*!)
Gentiana amarella L. var. *acuta* (Michx.) Herder, in Acta Hort. Petrop. 1:428. 1872.
Gentiana amarella L. var. *tenuis* (Griseb.) A. Gray, Syn. Fl. N. Amer. ed. 2, 2^1:118. 1886.
Gentiana anisosepala Greene, Pittonia 3:309. 1898. (*Heller & Heller 3440*!)
Gentiana acuta Michx. ssp. *acuta* Wettst. in Oesterr. Bot. Zeitschr. 50:290. 1900.
Gentiana acuta Michx. ssp. *plebeja* (Cham.) Wettst. loc. cit. 194. 1900.
Gentiana acuta Michx. ssp. *plebeja* f. *holmii* Wettst. loc. cit. 195. 1900. (based on *G. acuta* var. *nana* Engelm.)
Gentiana acuta Michx. var. *strictiflora* Rydb. Mem. N. Y. Bot. Gard. 1:309. 1900. (based on *G. acuta β stricta* Griseb.)
Gentiana stricta (Griseb.) Howell, Fl. N.W. Amer. 1:445. 1901.
Gentiana strictiflora (Rydb.) A. Nels. in Bot. Gaz. 34:26. 1902.
Gentianella clementis Rydb. in Bull. Torr. Bot. Club 31:631. 1904. (T.: *Clements & Clements 253*!)
Amarella anisosepala (Greene) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Amarella conferta Greene, loc. cit. 55. 1904. (T.: *Spreadborough s. n.*!)
Amarella copelandi Greene, loc. cit. 53. 1904. (T.: *Copeland s. n.*!)
Amarella lemberti Greene, loc. cit. 54. 1904. (T.: *Lembert s. n.*!)
Amarella macounii Greene, loc. cit. 54. 1904. (T.: *Macoun s. n.*!)
Amarella revoluta Greene, loc. cit. 55. 1904. (T.: *Wooton 552*!)
Amarella strictiflora (Rydb.) Greene, loc. cit. 53. 1904
Amarella tenuis (Griseb.) Greene, loc. cit. 53. 1904.
Amarella amarella (L.) Cockerell, in Am. Nat. 40:871. 1906.
Amarella plebeia var. *holmii* (Wettst.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.
Amarella gurliae Lunell, in Am. Midl. Nat. 2:142. 1911. (T.: *Lunell 816*!)
Amarella theiantha Lunell, loc. cit. 143. 1911. (T.: *Lunell 818*!)
Amarella theiantha Lunell var. *livida* Lunell, loc. cit. 142. 1913. (T.: *Lunell 820*!)
Amarella theiantha Lunell var. *lactea* Lunell, loc. cit. 1913. (T.: *Lunell 819*!)
Gentiana amarella L. f. *michauxii* Fern. in Rhodora 19:151. 1917. (based on *G. acuta* Michx., sensu stricto)
Gentianella acuta (Michx.) Hiit. in Mem. Soc. Faun. Fl. Fenn. No. 25:76. 1950.

Newfoundland, Maine and Vermont, westward to Alaska, southward in the western mountains to Baja California and central Mexico.

Some of the large number of reported habitats with flowering dates and elevations, are as follows:

Alaska: Rocky shores, sand-dunes, sea-beaches, tundras, lake shores, moist grassy swales, apparently at rather low altitudes; flowering and fruiting from June to September.

Alberta: Roadsides, open poplar woods, alkaline meadows, dry prairies, mountain slopes, sides of coulees; late July until September.

Quebec: Wet fields, calcareous gravel, limestone, turfy slopes, sandy headlands, above the tide mark, near sea-level; late June to early September.

Wyoming: Along creeks, open woods, alpine meadows, alkali areas up to 3000 meters; late July and throughout August.

California: Grassy banks, poplar woods, grassy places in yellow pine forest, to 2500 meters; early June to September dependent upon altitude.

Arizona: Dry or moist meadows to 3500 meters; flowering and fruiting from mid-August until September.

CANADA:

ALBERTA: Lake Louise, *Brown 546* (GH, MO, PH, US); Bow Lake, Banff Nat. Park, *Hitchcock & Martin 7791* (plants 1, 3, 4, 6, & 7 GH); Banff to Field, *Schaffer s. n.* (PH); Cypress Hills, Spring Creek, *Breitung 5518* (DAO, MO); Elkwater Lake, *Breitung 5547* (DAO); Craigmyle District, *Brinkman 267* (NY), *292* (DAO); Twin Butte, *Gillett 6023* (DAO); Keg River, *Groh 2934* (DAO); Mt. Temple, Loggan, *Butters, Holway & Rosendahl 305* (GH, NY, US); Pincher Creek, *Gillett 6026* (DAO); Waterton Lakes Nat. Park, *Gillett 6029* (DAO); Crow's Nest Pass, *Macoun s. n.* (US); Wood Buffalo Park, Moose (Eight) Lake, *Raup 3030* (CAN, GH, US), *3031* (CAN); Hay Camp Dist. Slave River, *Raup 3032* (CAN, GH); Brasean, headwaters Saskatchewan and Athabasca rivers, *Brown 1435* (GH, MO, PH); Fort Chipewyan, *Raup 7028* (GH); Jasper Nat. Park, *Riley 6* (US); Devona, *Scamman 3153* (GH, US); Fort Saskatchewan, *Turner 2118* (DAO); Beaverlodge, *Lindsay 303* (DAO); Grande Prairie, *Malte 40* (CAN); Edmonton, *Malte s. n.* (CAN); Caribou Mountains, *Raup 3035* (CAN); Rosedale, *Moodie 1209* (F); Peace River, Indian Graveyard, *Raup 3036* (CAN); Lake Mamawi, *Raup 3037* (CAN).

BRITISH COLUMBIA: Victoria, *Fletcher s. n.* (DAO); Apex Mountain near Hedley, *Gillett & Senn 6053* (DAO); Prince George, *Groh 636* (DAO); Hudson Hope, Peace River Dist., *Groh 745* (DAO); Skaget, *Davidson s. n.* (UBC); Victor Lake, near Revelstoke, *Hitchcock & Martin 7575* (GH, NY, WS); Kettle and Columbia rivers, *Macoun*

s. n. (WS); Cassiar Dist., Telegraph Creek, *Preble & Mixter 577* (US); Mt. Robson, *Scammon 3322* (GH, US); Selkirk Mts., *Shaw 180* (GH, MO, US, WS); Caribou, 150 Mile House, *Wilson 717* (UBC); Foghorn Mt. s. of Waverly, *Tisdale s. n.* (DAO); Tranquille Range, Kamloops, *Tisdale 40-621* (DAO); Elk River, Natal, *Weber 2301* (WS); nr. Cranbrook, *Calder & Savile 9169* (DAO); Okanagan, Allen Grove, *Copley 22* (UBC); between Moyie & Cranbrook, *Eastham 15373* (UBC); Fermie, *Eastham 15695* (UBC); Colleymount, François Lake, *Eastham 11907* (UBC); Anahim Lake, Chilcoten, *Cornwall s. n.* (UBC); Paradise Mine, Windermere, *Calder & Savile 11300* (DAO); Takakkaw Falls, Yoho River Valley, *Calder & Savile 12016* (DAO); Chute Lake, Naramata, *Calder & Savile 10202* (DAO); Cascade, *Calder & Savile 9539* (DAO); Quesnel, *Taylor s. n.* (UBC); Fairmont Hot Springs, *Eastham 10137* (UBC); Williams Lake, Dog Creek Range, *Carlyle s. n.* (UBC); Queen Charlotte Islands, Massett, *Newcombe s. n.* (F); Nakina Lake, Atlin Dist., *Aitken 39* (DAO); Topley, *Calder, Savile & Ferguson 14535* (DAO); Wells, *Calder, Savile & Ferguson 14193* (DAO); Kispiox River, n. Hazelton, *Calder, Savile & Ferguson 14751* (DAO); Azouzetta Lake, *Calder, Savile & Ferguson 13996B* (DAO); Ft. St. James, *Calder, Savile & Ferguson 13622* (DAO); Mt. Pope, *Calder, Savile & Ferguson 13799* (DAO); Hudson Bay Mountain, Smithers, *Calder, Savile & Ferguson 14668* (DAO).

LABRADOR: Blanc Sablon, Straits of Belle Isle, *Fernald & Wiegand 3905* (GH); Cartwright, *Hitchcock 23845* (US); L'Anse au Clair, *Waghorne 2* (US).

MACKENZIE DISTRICT: Lac Ste. Croix and Bear Lake, *Preble 268* (US); Fort Smith, *Preble & Preble 171* (US); Yellowknife, *Cody & McCanse 3246* (DAO); Little Buffalo River, *Loan 327* (DAO); Seven Mile Lake, *Cody & Loan 4661* (DAO).

MANITOBA: Lyleton, *Boivin & Breitung 6588* (DAO); Turtle Mt., *Burgess s. n.* (DAO); Brandon, *Macoun s. n.* (F); Winnipeg, *Denike 1689* (DAO); Wabowden Lake, Mile 137 Hudson Bay R.R., *Gillett 2775* (DAO); Dauphin, *Groh s. n.* (DAO); Stony Mountain, *Groh s. n.* (DAO); Riding Mountain Nat. Park, *Rowe 60A* (DAO); Cartwright, *Senn & Gordon 3036* (DAO); Broomhill, *Senn & Gordon 3120* (DAO); Melita, *Senn & Gordon 3102* (DAO); Chaplin, *Spreadborough s. n.* (ND).

NEW BRUNSWICK: Gloucester Co.: Grande Plaine, Miscou Island, *Blake 5594* (GH, US), *Ganong s. n.* (GH); Goat Island, mouth of St. John River, *Hay s. n.* (PH).

NEWFOUNDLAND: Cartierville, *Bassett 715* (DAO); St. Barbe, *Fernald, Long, et al. 26972* (GH, PH); Ingornachoix Bay, *Fernald & Wiegand 3902* (GH, PH); St. Anthony Bight, *Savile 2925* (DAO); St. John Bay, Bard Harbour, *Wiegand & Gilbert 28931* (GH, PH).

ONTARIO: Schreiber, Lake Superior n. shore, *Dore 9236* (DAO); St. Ignace Islands, Lake Superior, *Smith s. n.* (PH).

QUEBEC: Fort Chimo, *Calder 2412* (DAO, US); Anticosti, Baie Sainte-Claire, *Victorin 4290* (MO, US); Rivière au Saumon, *Victorin et al. 21064* (F); Bonaventure Co.: *Williams & Fernald s. n.* (US). Gaspé Co.: Paspebiac, *Churchill s. n.* (MO); James Bay, Fort George, *Lepage 12851* (DAO); Rupert House, *Spafford 160* (DAO); Temiscouata, *Pringle s. n.* (F, MO, PH, US); Douglastown, *Collins & Pease 6605* (F); Magdalen Islands, Coffin Island, *Fernald, Long & St. John* (PH, US, WS); Mingan Islands, Île de Sainte-Genevieve, *Victorin & Rolland 21063* (GH, MO, PH); Rivière du Loup, *Canby s. n.* (F).

SASKATCHEWAN: Springside, *Blaricom 26* (F); Carleton House to Cumberland House, *Drummond s. n.* (GH); Cypress Hills, Fort Walsh, *Breitung 5685* (DAO, MO); Moose Jaw, *Barber 30* (GH); Saskatoon, *Macoun & Herriot s. n.* (GH); Lake Athabasca, *Raup 6591* (GH); Regina, *Cowdry s. n.* (DAO); Watrous, *Sallans & Russell s. n.* (DAO); Yorktown, *Shaw 157* (DAO); Sutherland, *Russell s. n.* (DAO); McKague, *Breitung 476* (DAO); Invermay, *Russell S1794* (DAO); St. Louis, *Senn, Groh & Russell 2838* (DAO); Manitou Lake, *Frankton & Bibbey 413* (DAO); Bjorkdale, *Laycock s. n.* (DAO); Prince Albert, *Senn, Groh & Russell 2817* (DAO); Willowbunch, *Gillett & Boivin 6013* (DAO); Bengough, *Gillett & Boivin 6010* (DAO); Whitewood, *Gillett & Boivin 6001* (DAO); Ile à la Cross, Churchill River, *Breitung 8427* (DAO); Kennedy, *Gillett & Boivin 6002*; Macdowall, *Senn, Groh & Russell 2898*, (DAO); Rockglen, *Gillett & Boivin 6018* (DAO).

YUKON: Dawson, *Macoun s. n.* (NY); Bear Creek near Lake Desert d'Asch, *Müller s. n.* (PH, US).

United States:

alaska: Fort Yukon, *Kennicott s. n.* (F); Hiulink, *Harrington s. n.* (US); Unalaschka, *Harrington s. n.* (MO); Fairbanks, *Palmer 1826* (US); Spruce Island, *Kellogg 246* (PH, US); Juneau, *Cowles 1096* (F, GH, MO, US); Karluk, Kodiak Island, *Rutter 71* (GH, NY, US); Homer, *Evans 499* (US); Dutch Harbor, Unalaska Island, *True & Prentiss 129* (US); Lake Kenai, Kenai Peninsula, *Calder 5587, 6335* (DAO); Cape Phipps, *Funston 72* (F, GH, MO, US); Katmai Region, Alaska Peninsula, *Hagelbarger 165* (US); Attu Island, Sarana Bay, *Van Schaack 1000* (MO, US); Behring Island, *Macoun s. n.* (US); Alitak, *Looff & Looff 774* (UBC); Adak Island, *Dorwart 45* (F); Dauer Bay, *Cooper & Andrews 313* (F).

arizona: Apache Co.: White Mts., *Eggleston 15771* (F, GH). Coconino Co.: Kaibab Forest, Grand Canyon Park, *Kearney & Peebles 13727* (US). Graham Co.: Pinaleno Mts., Darrow, *Phillips & Putz 1106* (US). Yavapai Co.: *Lemmon 4200* (GH). Yuma Co.: Buckskin Mts., *Jones 6056n* (US).

california: Butte Co.: Butte Meadows, *Heller 14689* (MO, NY, US); Jonesville, *Copeland 441* (F). Inyo Co.: Whitney Meadows, *Coville & Funston 1631* (US). Mariposa Co.: Tuolumne, Yosemite Nat. Park, *Heller 15464* (MO, NY, PH, US). Mono Co.: Bloody Canyon, *Chesnut & Drew s. n.* (US). Nevada Co.: *Williamson s. n.* (PH). Placer Co.: Summit Station, *Sonne s. n.* (US); Truckee, *Sonne 217* (F). San Bernardino Co.: Pine Lake, *Abrams 2897* (GH, MO, PH, US). Plumas Co.: *Austin s. n.* (US); Bear Lake, *Clokey 7000* (F). Shasta Co.: *Newberry s. n.* (US). Sierra Co.: *Lemmon 190* (NY). Siskiyou Co.: Mount Eddy, *Copeland s. n.* (ND). Tuolumne Co.: Tuolumne River, *Bolander 5045* (F, MO, NY, PH, US); Yosemite Valley, *Lembert s. n.* (ND). Tulare Co.: Kern River, *Greene 4241* (GH, NY).

colorado: Boulder Co.: Boulder, *Holzinger s. n.* (US). Chaffee Co.: Garfield, *Eggleston 6068* (GH, US). Clear Creek Co.: Georgetown, *Patterson 287* (F, GH, MO, US). Custer Co.: Wet Mountain Valley, *Horner s. n.* (GH). Denver Co.: *Glatfelter s. n.* (MO). Eagle Co.: Leadville Forest, *Eggleston 11842* (US). El Paso Co.: Minnehaha, *Clements & Clements 253* (GH, MO, NY, US); Pike's Peak, *Spruce s. n.* (F). Fremont Co.: Grape Creek, *Demitrio s. n.* (GH). Garfield Co.: White River Plateau, *Hermann 5580* (MO). Gilpin Co.: Black Hawk, *Sheldon 286* (PH, US). Grand Co.: Berthoud Pass, *Clokey & Clokey 4241* (CAN, MO, UC, US, WS). Gunnison Co.: Gunnison, *Baker 600* (GH, MO, US, WS). La Plata Co.: Durango, *Baker et al. 629* (MO, NY, US). Routt Co.: Steamboat Springs, *Crandall s. n.* (US). Hinsdale Co.: Lake City, *Pease s. n.* (NY). Jackson Co.: Lake John, *Shear & Bessey 4335* (US). Jefferson Co.: Golden, *Greene s. n.* (GH). Lake Co.: Twin Lakes, *Clokey 2548* (CAN, MO, NY, US, WS). Larimer Co.: Chamber's Lake, *Baker s. n.* (MO, NY, US). Mineral Co.: *Murdock 4842* (MO, NY). Ouray Co.: Ouray, *Evermann s. n.* (US). Park Co.: Jefferson, *Cowen 1502* (CAN, US, WS). Pitkin Co.: Sawatch Range, *Brandegee s. n.* (MO). Rio Blanco Co.: North Elk Canyon, *Sturges s. n.* (GH). Rio Grande Co.: Del Norte, *Evermann s. n.* (US). Saguache Co.: Marshall Pass, *Baker 885* (GH, MO, US). San Juan Co.: Head of Vallecito, *Knowlton 44* (US). San Miguel Co.: Trout Lake, *Payson & Payson 4117* (GH, MO). Summit Co.: Breckenridge, Mt. Guyot, *Anderson s. n.* (MO). Location unknown: *Parry 309* (GH, MO, NY).

idaho: Blaine Co.: Hyndman Creek, *Thompson 13520* (PH, MO, US, WS). Boise Co.: Warm Springs Creek, *Woods & Tidestrom 2709* (US). Boundary Co.: Hughes Fork Trail, *Warren 368* (WS). Custer Co.: Bonanza, *Macbride & Payson 3475* (GH, MO, US). Fremont Co.: Henry's Fork, *Coulter s. n.* (PH, US). Kootenai Co.: Lake Cœur d'Alene, *Aiton s. n.* (F, MO, US). Latah Co.: Cedar Mts., *Sandberg & MacDougal 424* (F, GH, MO, PH, US); Moscow Mountain, *Baker 134* (ID), *Thomas s. n.* (ID). Lemhi Co.: Challis, *Hitchcock & Muhlick 11346* (GH, NY, US, WS). Nez Perce Co.: Forest, *Heller & Heller 3440* (DAO, MO, ND, NY).

maine: Aroostook Co.: St. John River, Van Buren, *Fernald s. n.* (GH); St. John River, St. Francis, *Fernald 85* (CAN, F, GH, MO, PH, US); Houlten, *Fubish s. n.* (GH).

montana: Beaverhead Co.: Pioneer Range, *Hitchcock & Muhlick 13030* (GH, MO, UC, WS). Carbon Co.: Red Lodge, *Hitchcock & Muhlick 13554* (WS). Flathead Co.: Big Fork, *Jones s. n.* (GH, MO, US). Gallatin Co.: Gallatin Canyon, *Blankinship 349* (PH, US); Glacier Co.: 3 mi. s. Babb, *Daubenmire 48381* (WS); Glacier Nat. Park,

Bowman, *Evans s. n.* (F). Granite Co.: Garnet, *Scheuber s. n.* (NY). Lake Co.: Big Fork, *Clemens s. n.* (GH). Lewis & Clark Co.: Flathead Nat. Forest, *Hitchcock 18743* (WS). Madison Co.: Ennis, *Hitchcock 16736* (UC, WS). Meagher Co.: Martinsdale, *Canby s. n.* (F, PH, MO). Missoula Co.: Woodman, *Kirkwood 1475* (GH). Park Co.: Wilsall, *Suksdorf 87* (GH, WS). Powell Co.: Flathead Nat. Forest, *Hitchcock 18549* (ID, WS). Sweet Grass Co.: MacLeod, *Pope 105* (NY). Teton Co.: Glacier Nat. Park, *Hunnewell 2158* (GH).

NEVADA: Elko Co.: Ruby Valley, *Heller 9467* (US).

NEW MEXICO: Catron Co.: Mogollon Peak, *Eggleston 16931* (US), *Rusby 262* (F). Colfax Co.: Castle Rock, *Wooton s. n.* (US). Lincoln Co.: White Mts., *Wooton 552* (MO, US). Sandoval Co.: Jemez Mts., *Bailey 1026* (US). San Miguel Co.: Pecos, *Standley 5011* (GH, MO, US). Santa Fe Co.: *Bertaud 24* (US). Taos Co.: Carson Forest, Apache Peak, *Eggleston 19200* (US).

NORTH DAKOTA: Benson Co.: Leeds, *Lunell 816* (MIN, NY), *Lunell 818* (MIN); Butte, *Lunell 820* (MIN). Bottineau Co.: Turtle Mts., *Stevens 540* (DAO, MO, US). Divide Co.: Fortima, *Metcalf 597* (US). McHenry Co.: Tower, *Lunell 819* (MIN).

OREGON: Crook Co.: Pengra, *Coville & Applegate 541* (US). Deschutes Co.: Big Meadows, *Leiberg 496* (GH, MO). Jefferson Co.: Metoline River, *Gorman 3887* (WS). Klamath Co.: Fort Klamath, *Peck 9557* (MO, PH). Union Co.: Blue Mts., *Cusick 1029* (GH, US); Wallowa Mts., *Cusick 2101* (F, MO, US, WS).

SOUTH DAKOTA: Custer Co.: Custer, *Degener & Peiler s. n.* (MO, US). Lawrence Co.: Lead, *Carr 144* (DAO, GH, MO). Pennington Co.: Redfern, *Murdoch 4285* (GH, US); Mystic, *Visher s. n.* (F).

UTAH: Beaver Co.: Tashar Mts., *Eggleston 10417* (US). Cache Co.: Tony Grove Lake, *Maguire 16996* (WS). Duchesne Co.: Krobs Basin, *Hermann 5190* (GH, MO). Garfield Co.: Aquarius Plateau, *Ward 440* (MO, US). Kane Co.: *Siler s. n.* (MO). Salt Lake Co.: Brighton, *Maguire 17317* (US, WS). Sanpete Co.: *Watson 59* (ID). Sevier Co.: Fish Lake, *Jones 5823* (GH, MO, NY, US, WS). Washington Co.: Springdale, *Jones 6078* (MO).

VERMONT: Lamoille Co.: Mt. Mansfield, Smuggler's Notch, *Pringle in 1871* (MO, NY, PH, US); and many other collections in most American herbaria.

WASHINGTON: Clallam Co.: Mt. Angeles, *Thompson 7357* (GH, MO, PH). Ferry Co.: Coville, *Hitchcock 17607* (DAO, ID, US). Jefferson Co.: Olympic Mts., Marmot Pass, *Thompson 7988* (GH, MO, PH). King Co.: Seattle, *Freiberg s. n.* (MO). Okanogan Co.: Salmon Meadows, *Thompson 6943* (GH, MO). Pend Oreille Co.: *St. John 6462* (WS). San Juan Co.: Friday Harbor, *Zeller & Zeller 918* (GH, MO, US). Skagit Co.: Dewey, *Mason s. n.* (WS). Stevens Co.: Arden, *Spiegelberg 267* (WS). Whatcom Co.: Padden Lake, *Suksdorf 990* (F, GH, MO, US, WS).

WYOMING: Yellowstone Nat. Park, Snake River, *Nelson & Nelson 6447* (GH, MO, US, WS). Albany Co.: Centennial, *Nelson 8803* (GH, MO, US). Big Horn Co.: Middle Ten Sleep Creek, *Goodding 471* (GH, US). Carbon Co.: Rawlins, *Goodding 570a* (MO, US). Park Co.: Beartooth Lake, *Williams & Williams 3755* (GH, MO, NY). Shoshone Co.: 21 mi. from Cooke City, *Iltis 3996* (DAO). Sheridan Co.: Spring Creek, *Williams & Williams 3362* (GH, MO, NY). Sublette Co.: Surveyor Park, Fremont Lake, *Payson & Payson 2903* (GH, MO, US). Teton Co.: Teton Mts., *Porter 4741* (DAO). Uinta Co.: Mt. View, *Maguire, Piranian & Richards 12643* (GH). Washakie Co.: Big Horn Mts., *Porter 4343* (GH, MO). Weston Co.: Newcastle, *Nelson 2551* (F).

MEXICO:

BAJA CALIFORNIA: La Sanca Creek, 5 mi. n.w. La Grulla Sierra, San Pedro Martir, *Wiggins & Demaree 4845* (F, GH); La Encantada nr. Vallecitos, Sierra San Pedro Martir, *Wiggins 9075* (GH, US).

MÉXICO: Nevada de Toluca, *Moore 89a* (GH), *Kenoyer s. n.* (F).

NUEVO LEON: Municipio de Galeana, peak of Cerro Potosi, *Schneider 971* (F, GH), *Mueller 2247* (F, GH).

For the combination *Gentianella amarella* (L.) Börner and other Börner references I am indebted to Dr. Harald Smith, of Uppsala, who pointed out to me that Börner had made the combination earlier in his Flora. This Flora, although recent, is not widely distributed on this side of the Atlantic. The Library of Congress has a copy but I know of no other in the United States.

G. amarella ssp. *acuta* is extremely variable, particularly in the number of internodes, the size and shape of the calyx lobes, the length of the corolla tube and lobes, and the density of the inflorescence. Field observations indicate that great variability in height of the plant, density of the inflorescence, color of the flowers, and other features is found in local populations as well as in groups of plants of the range as a whole. The pattern of this variability is not sufficiently well understood at this time to warrant the recognition of additional forms or subspecies.

It has been necessary to establish the relationship of ssp. *acuta* to the European population of *Gentianella amarella* (*sensu lato*). The few European specimens of *G. amarella* that I have seen show an astonishingly great variability. Many "species" have been based upon the variants of this European population; many of them are difficult to distinguish morphologically, and perhaps should be reduced to subspecific or lesser rank. Most of the typical specimens of the European *G. amarella* have somewhat larger flowers than do the American plants of ssp. *acuta*. Since *G. amarella* does not occur in Greenland, the American and the European populations are disjunct. Because of this geographic disjunction and the difference in flower size, I am recognizing the American population as subspecifically distinct from typical *G. amarella* of Europe.

The few specimens I have seen from Siberia and other parts of Asia show close resemblance to *G. amarella* ssp. *acuta*. These Asiatic plants have been described under the name *Gentiana ajanensis* by Murbeck.[60] However, I shall not consider the Asiatic population as synonymous with ssp. *acuta* until I have seen more material from that region.

11c. GENTIANELLA AMARELLA (L.) Börner, ssp. **mexicana** (Griseb.) J. M. Gillett, comb. & stat. nov.

Gentiana mexicana Griseb. Gen. & Sp. Gent. 243. 1839, ex char. (T.: *Schiede s. n.*)
Amarella mexicana (Griseb.) Arthur, in Torreya 12:34. 1912.

Southern and central Mexico; in wet meadows and on gravelly slopes near timber-line and along creek banks at elevations of 2000–3000 meters. Flowering from mid-September through October; fruiting in October and November.

MEXICO:

FEDERAL DISTRICT: south of Contreras, *Russell & Souviron 197* (US); Desierto de los Leones, *Lyonnet 517* (GH, MO, NY, US); La Cima, 9800 ft., *Barnes & Land 383* (F). HIDALGO: Pachuca District, Mineral del Chico, Parque Nacional El Cluco, *Moore 1607* (GH).

MEXICO: Temascaltepec, *Hinton 8313* (F, GH, MO, NY, US); Crucero-Agua Blanca, Temascaltepec, *Hinton 8330, 2117* (F, GH, MO, NY, US); Sierra de las Cruces, *Pringle 4277* (F, MO, NY, PH, US).

[60] Murbeck, in Acta Hort. Berg. 2^3:1–28. 1892.

OAXACA: Sierra de Calvellinas, 9000 ft., Smith *667* (MO, US).
PUEBLA: Ixtaccihuatl, *Purpus 1757* (F, MO, US).
VERACRUZ: Cofre de Perote, 9300 ft., *Balls 5435* (US).
LOCALITY UNKNOWN: *Ehrenberg 79* (GH).

11d. GENTIANELLA AMARELLA (L.) Börner, ssp. **sandiana** J. M. Gillett, subsp. nov.

Plantae 2.0–3.5 dm. altae ramosae. Folia basalia elliptica vel spatulata 4–10 mm. longa jam marcida superiora ovata vel ovato-lanceolata, 10–25 mm. longa 5–10 mm. lata, acuta. Flores numerosi, 9–17 mm. longi, aut infundibuliformes aut hypercrateriformes cum lobis maxime dilatatis sessiles aut pedicellis ca. 8 mm. longis in cymis terminalibus axillaribusve dense aggregatis umbelliformibus vel corymbiformibus. Calix 5–17 mm. longus, tubo 2.0–2.8 (–3.0) mm. longo, lobis lineari-oblongis acutis subaequalibus quam tubo aliquantum longioribus sinibus rotundatis margine minute denticulato. Corolla alba 10–15 mm. longa lobis albis aut purpureo-maculatis basim fimbriatis. Anthera 1 mm. longa 0.5 mm. lata. Ovarium sessile ca. 12 mm. longum 1.5 mm. latum; stigmata oblonga patula vel erecta ca. 0.5 mm. longa. Semina immatura rotundata laevia maturitate ignota.

Restricted to Chihuahua and Durango. Habitat probably similar to that of *G. wislizeni* for some material is from the same locality. At an altitude of about 2500 meters, flowering in October.

MEXICO:
CHIHUAHUA: *Palmer 334* (GH, NY, US); 65 mi. east of Batopilas, *Goldman 188* (US).
DURANGO: Mesa de Sandia, *Pringle 10111* (F, GH, MEXU, MO HOLOTYPE, NY, US).

Very similar to *G. wislizeni* in many respects but having a distinctly tubular calyx. The dense terminal corymbs of fimbriate flowers with the speckled corolla lobes are striking features of this subspecies.

11e. GENTIANELLA AMARELLA (L.) Börner, ssp. **wrightii** (A. Gray) J. M. Gillett, comb. & stat. nov.

Gentiana wrightii A. Gray, Syn. Fl. N. Amer. ed. 2, 2^1:118. 1886. (T.: *Wright 1659!*)
Amarella wrightii (A. Gray) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.
Amarella cobrensis Greene, loc. cit. 56. 1904. (T.: *Greene s. n.!*)
Gentiana townsendii Briq. in Candollea 4:329. 1931. (T.: *Townsend & Barber 358!*)

Northern Mexico and in adjacent New Mexico; flowering from late August until the middle of November, at altitudes of 2100–2400 meters, in moist and springy places.

UNITED STATES:
NEW MEXICO: Grant Co.: Pinos Altos Mts., *Greene s. n.* (F, MO, NY, PH).
MEXICO:
CHIHUAHUA: Sierra Madre, *Jones s. n.* (MO, US); southwest Chihuahua, *Palmer 306* (F, GH, MO, US); near Colonia Garcia, *Townsend & Barber 358* (F, GH, MO, NY, US); *Pennell 18744, 19116* (US).
SINALOA: Cerro del Viejo, San Ignacio, *Montes & Salazar 83* (US).
SONORA: Santa Cruz, *Wright 1659* (GH, MO, NY, PH, US).
LOCALITY UNKNOWN: Cima, *Orcutt 3800* (F).

Subspecies *wrightii* is extremely variable. Greene's *Amarella cobrensis* is very similar to the material collected by Wright. *Gentiana townsendii* appears to be but a form with exceptionally dense axillary inflorescences. Since so little material of *G. townsendii* is available, I do not feel that much significance can be attached to this variation, because the flowers appear to be identical in every respect to other sheets of ssp. *wrightii.*

Gentianella amarella ssp. *hartwegii* and *G. amarella* ssp. *wrightii* are related to the more northern *G. amarella* ssp. *acuta*, but are distinguishable quite easily by the longer calyx tube and the nature of the lobes. The calyx lobes of ssp. *acuta* are thin, as are those of ssp. *wrightii*, and the margins are little differentiated from the central part of the lobe. In ssp. *acuta* the midrib of each lobe is not prominent and appears as a thin nerve. In ssp. *hartwegii*, however, the lobes are somewhat coriaceous, the margins somewhat thickened, and the midrib of each lobe broad and papillose, forming a flattened keel which extends the length of the calyx tube and is paralleled by a similar keel proceeding from the sinus. The midribs of the calyx lobes of ssp. *wrightii* are intermediate between those of ssp. *acuta* and ssp. *hartwegi.*

11f. Gentianella amarella (L.) Börner, ssp. **hartwegii** (Benth.) J. M. Gillett, comb. nov.

Gentiana hartwegi Benth. Pl. Hartw. 47. 1840. (T.: *Hartweg 351*, photo MO!)
Gentiana citrina Pollard, in Proc. Biol. Soc. Wash. 13:130. 1900. (T.: *Pringle 4196*!)
Gentiana mexicana Griseb. ssp. *hartwegi* (Benth.) Wettst. in Oesterr. Bot. Zeitsch. 50:291. 1900.
Gentiana mexicana ssp. *hartwegi* f. *pringlei* Wettst. loc. cit. 291. 1900. (T.: *Pringle 4237*!)
Amarella hartwegi (Benth.) Arthur, in Torreya 12:33. 1912.

In the states of Mexico and Michoacan, Mexico; in wet mountain meadows at altitudes of 2800–3300 meters; flowering from mid-August until October; fruiting in October and November.

Mexico:

mexico: Nevado de Toluca, *Kenoyer A357* (F); Temascaltepec, *Hinton 1317, 8320* (F, GH, MO, US); Valley of Toluca, *Pringle 4196* (F, GH, MEXU, MO, NY, US), *Pringle 4237* (F, GH, MO, US); Desierto Vieja, Valée de Mexico, *Bourgeau 1125* (GH).
michoacan: Angangueo, *Hartweg 371* (NY, photo F, MO).
locality unknown: *Sessé, Mociño, Castillo & Maldonado 684, 1370* (F).

Wettstein considered ssp. *hartwegii* a subspecies of *G. mexicana*. While all of the Mexican plants are very closely related I believe that ssp. *mexicana* is more closely allied to ssp. *acuta* than to ssp. *hartwegii*. Subspecies *hartwegii* has flowers that are very similar to those of ssp. *wrightii*, but differs in habit and range. Wettstein's *Gentiana mexicana hartwegi* forma *pringlei* is a high-altitude form, but in some duplicates of the Pringle type collection the plants are as large as the so-called "low-elevation" form. With the little material available it would be futile to segregate smaller plants of higher elevations. My own field experience with other species is that in the plants of a continuous population reduction in size regularly occurs at higher altitudes.

12. GENTIANELLA **auriculata** (Pall.) J. M. Gillett, comb. nov.

Gentiana auriculata Pallas, Fl. Ross. 1^2:102, *t. 92, f. 1.* 1788, ex char. & ic.
Dasystephana auriculata (Pall.) Borckh. in Roem. Archiv f. Bot. 1^1:26. 1796.
Hippion auriculatum (Pall.) Schmidt, in Roem. loc. cit. 11. 1796.
Amarella auriculata (Pall.) Greene, Leafl. Bot. Obs. & Crit. 1:53. 1904.

Caulescent annuals (?), 2–25 cm. tall, simple or branched, occasionally from the base, more frequently above. Basal leaves forming loose rosettes, obovate-spatulate to elliptic, the apex rounded or obtuse, the base attenuate, 4–30 mm. long, 1–13 mm. wide; median and upper leaves elliptic-ovate to broadly ovate, obtuse to rounded, the base broadened and clasping, 8–40 mm. long, 3–15 mm. wide; the upper leaves very slightly smaller or equal to the median. Flowers axillary or terminal, in simple or aggregate cymes or occasionally solitary, the terminal flower conspicuously larger than the lateral, the terminal pedicels extremely variable, subsessile to 3.5 cm. long, the lateral equal to or correspondingly shorter than the terminal. Calyx 7–9 mm. long, 4- to 5-lobed (4-lobed in North America), the tube about 6 mm. long; lobes about equal, or either the inner or the outer pair broader than the others, strongly and reticulately veined, broader than long, about one-third the length of the tube, the margins entire or minutely papillose, the base auriculate. Corolla blue, narrowly funnelform to salverform when the lobes are fully expanded, 18–28 mm. long, 5–8 mm. wide at the orifice; lobes ovate, ¼–⅓ the length of the tube, the tips obtuse to subacute, the sinuses acute and frequently concealed by the imbrication of the lobes, the tube provided with a faucal corona, the fimbriae united at the base to form a lacerate squamella extending across the base of each lobe; interstaminal glands inconspicuous and extremely small, scutiform, at the very base of the corolla tube. Stamens slightly exserted; filaments inserted about the middle of the corolla tube, the wings about 1 mm. wide at the base, tapering gradually above; anthers oblong, 1.6–1.8 mm. long, about 1 mm. wide, versatile and attached near the middle. Pistil sessile, the ovary cylindrical, 15 mm. long, 1.5 mm. wide, tapering slightly near the tip; stigma sessile, oblong, 1.5 mm. long, 1.0 mm. wide, erect. Capsule slightly longer than the marcescent corolla, about 25 mm. long, dehiscing at the tip; seeds approximately ovoid, 0.75 mm. long, 0.6 mm. wide, smooth, minutely wrinkled under magnification, light brown.

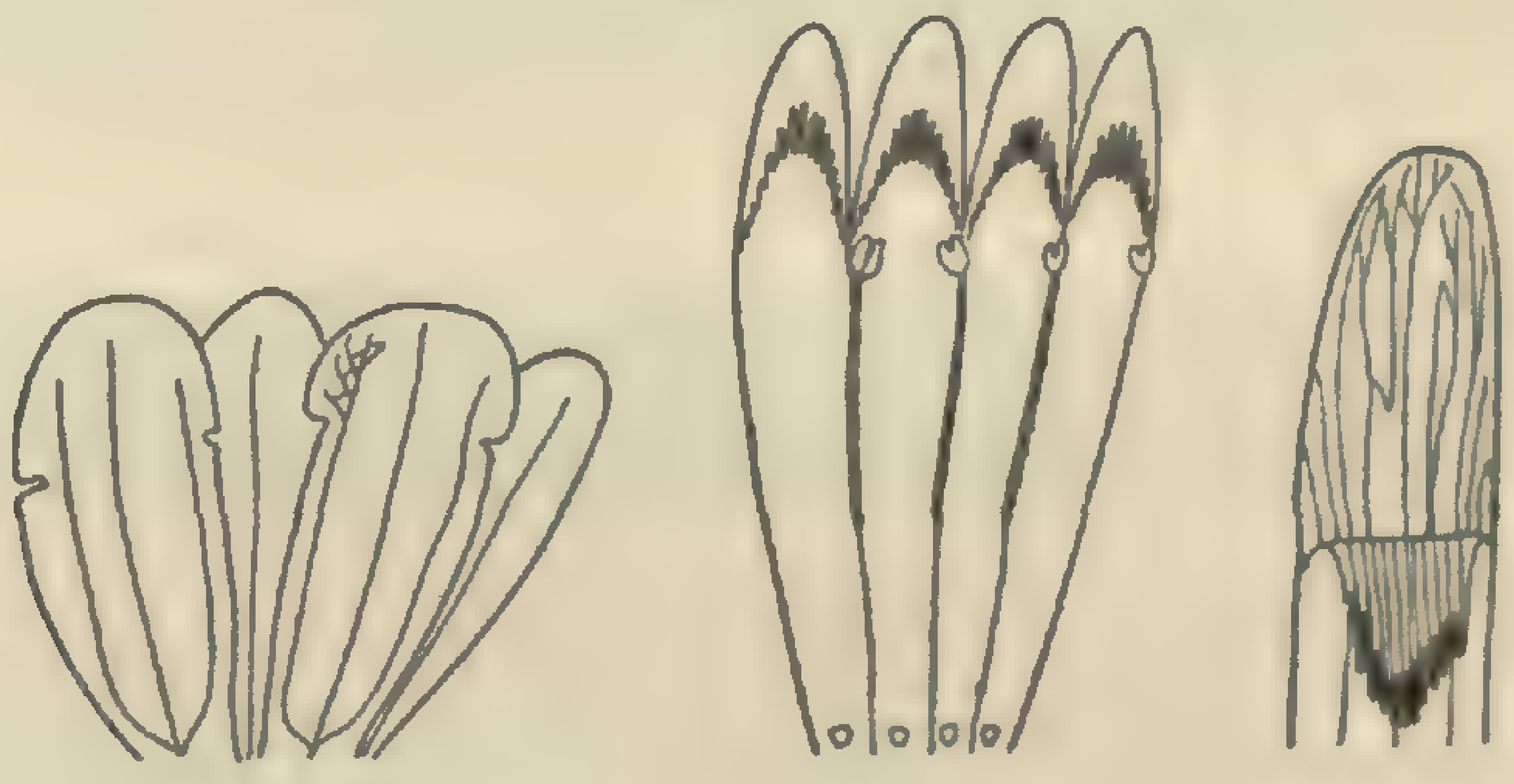


Fig. 8. Calyx (× 2), corolla (× 1), and corolla lobe of *Gentianella auriculata.*

On Attu Island, at the western extremity of the Aleutian Islands, on the Commander Islands in Behring Sea, in Kamchatka, on the islands north of Japan and about the Okhotsk Sea; on gravelly slopes at altitudes from sea level to 300 meters; flowering throughout August and presumably well into September; fruiting in September. Further habitat data are lacking since all Asiatic material examined gives no other information than the approximate location of the collection.

ALASKA: Aleutian Islands, Attu Island, vicinity of Massacre Bay, Lookout Hill, *Van Schaack 66* (MO, US), *748* (MO), *929* (MO, US).

The description has been based primarily on Kamchatkan and Japanese material since so little is available from North America. The excellent material from Attu Island collected by Van Schaack constitutes the only record of this plant from this continent. This fact has already been pointed out by Hultén in his flora. On a field label, Van Schaack notes that the specimens are 4-merous, while the material from Kamchatka and the Commander Islands is 5-merous. However, examination of more material shows that 4- and 5-merous material occurs both in Kamchatka and in the Commander Islands (Bering Island). As seen in other species the number of corolla or calyx lobes is a variable character, both types commonly occurring even on the same plant; indeed, in *G. aurea* and *G. amarella* ssp. *acuta* a 5-lobed calyx is frequently associated with a 4-lobed corolla.

SUBGENUS III. COMASTOMA (Wettst.) J. M. Gillett, stat. nov.

Gentiana sect. *COMASTOMA* Wettst. in Oesterr. Bot. Zeitschr. 45:174. 1896.
Lomatogonium A. Br. sect. *COMASTOMA* (Wettst.) Löve & Löve, in Acta Hort. Gotoburg. 20⁴:117. 1956.

Flowers 4- to 5-merous. Calyx tube short, the lobes foliaceous, sinuses lacking an inner membrane. Corolla 4- to 5-parted, the lobes ovate, entire, the orifice with two evascular fimbriate scales at the base of each lobe, the interstaminal glands epipetalous and in pairs. Stamens inserted slightly above the middle of the corolla tube, the anthers oblong, slightly longer than wide, the filaments minutely papillose. Ovary with several rows of ovules that frequently extend nearly to the center of the carpel wall. Seeds ovoid, somewhat flattened, smooth or slightly papillose at one end.

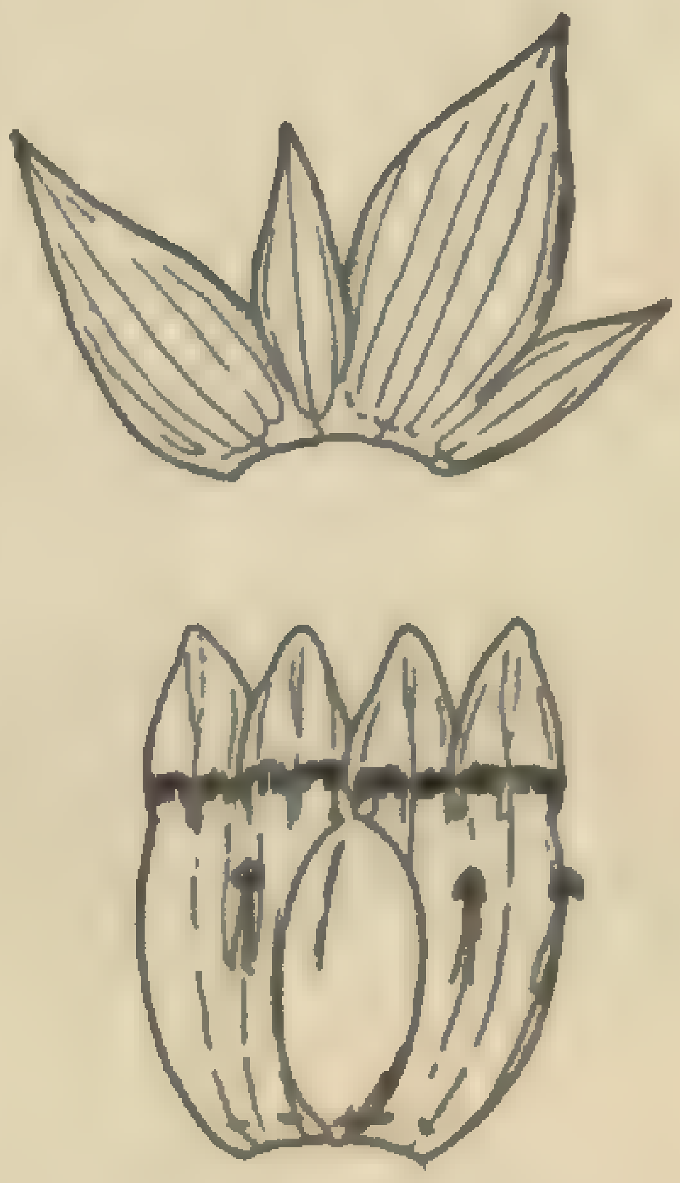
13. GENTIANELLA TENELLA (Rottb.) Börner, Fl. deut. Volk, 542. 1912. (*G. tenella* (Rottb.) H. Sm. ex Hylander, in Uppsala Univ. Arssk. 259. 1945, superfluous comb.)

Gentiana tenella Rottb. in Kiob. Selsk. Skrift. (Acta Hafn.) 10:436. 1770. (T.: *Collector unknown*, C!)
Lomatogonium tenellum (Rottb.) Löve & Löve, Acta Hort. Gotoburg. 20⁴:117. 1956.

Annuals 1–26 (usually about 6) cm. tall, loosely to densely cespitose or branching above, or simple, the branches curved-ascending. Basal leaves two or forming dense rosettes, frequently deciduous, elliptic, obovate to spatulate, 3–10 mm. long, 1–4 mm. wide, the apex rounded to obtuse, attenuate to the base; median and upper leaves ovate to ovate-elliptic, 4–9 mm. long, 1–3 mm. wide, the apex obtuse,

the base attenuate, somewhat clasping. Flowers solitary, terminal or axillary. Pedicels 2–10 cm. long. Calyx 4- to 5-merous, the tube nearly obsolete, 5–10 mm. long, the outer lobes foliaceous, broadly ovate to lanceolate, obtuse to acuminate, about 10 mm. long, 2–7 mm. wide, with or without an outer inflated saccate protrusion at the base, the inner lobes lanceolate, slightly shorter than the outer and about half to one-third as wide, the margins entire, the sinuses concealed by the imbrication of the lobes. Corolla blue to white, tubular to somewhat salverform, about 11 mm. long, 2–3 mm. wide at the orifice, the lobes oblong-ovate, imbricate, one-third to half as long as the tube, the tips obtuse, the orifice bearing at the base of the corolla lobe two groups of 4–6 blunt evascular fimbriae united at the base to form two fimbriate scales, or nearly free about half the length of the lobes, the interstaminal glands indistinct, appearing by transmitted light as two greenish, oblong stains about 1 mm. above the base of the tube. Stamens included, the filaments inserted near the upper third of the corolla tube, the wings about 0.3–0.4 mm. wide at the base, slightly tapering towards the anthers, the margins minutely papillose; anthers oval, about 1 mm. long, 0.5 mm. wide, versatile and attached near the middle. Pistil sessile; ovary fusiform, about 5 mm. long, about 1.5 mm. wide; stigmas sessile, ovate-oblong, 0.5 mm. long and wide, erect, the stigmatic surfaces facing inwards, recurving in fruit. Capsule longer than the marcescent corolla, up to 12 mm. long, dehiscing at the tip, the valves recurving about half their length. Seeds ovoid, slightly flattened, 0.75 mm. long, 0.5 mm. wide, the surface smooth, sub-papillose to papillose at one end, light brown.

A



B

Fig. 9. A, distribution of *Gentianella tenella* in North America. B, calyx and corolla of *G. tenella*, × 1¾.

Gentianella tenella occurs in northern Europe and Asia and in the mountains of the southern parts of those continents. In North America the species occurs in Greenland, northern continental Canada and Alaska; in the Rocky Mountains as far south as Arizona and New Mexico and in Mono County, California. Because the plants are small and inconspicuous they are often overlooked by collectors. This may explain the scattered distribution pattern. *G. tenella* grows in a variety of habitats from sandy sea beaches, moist and dry slopes, lake margins, wet meadows, rocky places, to alpine tundra, at altitudes from a few feet above sea level in the northern part of the continent to 3500 meters in the southern part; flowering from late July until late August or early September regardless of latitude; fruiting from late August until September.

KEY TO THE SUBSPECIES

a. Calyx lobes ovate to lanceolate; branches few; cauline leaves with evident internodes........ ....13a. *G. tenella* ssp. *tenella*

aa. One or two calyx lobes broadly ovate; branches numerous; stem leaves compacted by a shortening of the lower internodes. Pribilof Islands, Alaska...............13b. *G. tenella* ssp. *pribilofii*

13a. GENTIANELLA TENELLA (Rottb.) Börner, ssp. TENELLA

Gentiana koeningii Gunner, Fl. Norv. 2:102. 1772, ex char.
Gentiana glacialis Thom. ex Vill. Hist. Fl. Dauph. 2:532. 1787, ex char. (T.: *Hall 652*)
Gentiana tetragona Roth, Tent. Fl. Germ. 2:290. 1789, ex char.
Hippion longepedunculatum Schmidt, in Roem. Archiv f. Bot. 1:21. 1796, ex char.
Gentiana borealis Bunge, in Nouv. Mem. Soc. Nat. Mosc. 1:251. *t. 10. f. 2.* 1829, ex ic.
Cicendia tenella (Rottb.) Raf. ex Jacks. Ind. Kew. 1:533. 1893.
Gentiana monantha A. Nels. in Bull. Torr. Bot. Club 31:244. 1904. (T.: *Clements & Clements 456*!)
Amarella monantha (A. Nels.) Rydb. in Bull. Torr. Bot. Club 33:148. 1906.
Amarella tenella (Rottb.) Cockerell, in Amer. Nat. 40:871. 1906.
Gentiana tenella Rottb. var. *occidentalis* Rouss. & Raym. in Nat. Canad. 79:77. 1952. (T.: *Rousseau 200*!)
Gentiana tenella Rottb. var. *monantha* (A. Nels.) Rouss. & Raym. loc. cit. 77. 1952.
Gentiana tenella Rottb. var. *monantha* f. *alba* Rouss. & Raym. loc. cit. 79. 1952. (T.: *Duran 3105*!)

GREENLAND: Manby Peninsula, Blossville Coast, *Bartlett 311* (CAN, US); head of Muskox Fjord, *Seidenfaden 309* (C, NY, US); Geologfjorden, Stromdbergs Halvö, *Seidenfaden & Ostenfeld 369* (C, GH, NY); Julianehaab, Dist. Igaliko, *Porsild 8086* (CAN); Traill Island, *Sörensen 3274* (C, CAN), *3276* (C); Hudson Land, *Sörensen 5032* (C); Sondre Stromfjord, *Jensen s. n.* (C); *Porsild 8545* (CAN). Location unknown: Elvin, *Hartz s. n.* (C), *Jensen s. n.* (C), *Sabanse* (?), *Kruuse s. n.* (C); Hurry Inlet, *Kruuse s. n.* (C).

CANADA:

KEEWATIN DISTRICT: Southampton Island, *Brown 608* (DAO); Chesterfield Inlet, *Savile 1391* (DAO); Esquimo Point, *Marsh 62* (UT, photo CAN).

MACKENZIE DISTRICT: Coppermine, *Findlay 242* (DAO); west side Bathurst Inlet, Burnside River, *Kelsall & McEwan 182* (CAN).

YUKON TERRITORY: St. Elias Range, Mt. Turquat, *Bakewell 80*, & *150* (GH, fide Porsild).[61]

QUEBEC: Poste de Povugnituk, rive êst de la baie d'Hudson, *Rousseau 140*, & *200* (JBM); Baie Kayak dans l'estuaire de la baie Payne, *Rousseau 1496* (JBM).

[61] Porsild, in Nat. Mus. Can. Bull. 121:275. 1951.

UNITED STATES:

ALASKA: Nome, Seward Peninsula, *Scamman 3910* (GH), *Thornton 439* (US); Port Clarence, Teller, *Porsild & Porsild 1488* (CAN, GH); Unalaklet, *Porsild & Porsild s. n.* (CAN, GH, US); Kotzebue Sound, *Eschscholtz s. n.* (US); Kotzebue, *Lepage 25404* (CAN, DAO), *Scamman 4064* (GH).

ARIZONA: Coconino Co.: San Francisco Mts., *Knowlton 131* (US).

CALIFORNIA: Mono Co.: Bloody Cañon (Mono Pass), *Congdon Herb.* (GH); White Mts., McAfee Meadow, *Duran 2816* (F, GH, MO, NY, US).

COLORADO: Clear Creek Co.: near Empire, *Patterson 245* (C, GH, MO, NY, US). Clear Creek-Summit Cos.: Mount Flora, *Parry s. n.* (GH, MO, US); Gray's Peak, *Patterson s. n.* (MO, US), *Patterson & Beatty s. n.* (F, US). Gilpin Co.: James Peak, *Cox 233* (F, MO), *Fuller s. n.* (MO). Grand Co.: Lulu Pass, *Clokey et al. 4239* (NY, US, WS). Larimer Co.: Long's Peak, *Holm s. n.* (MO). Saguache Co.: Cristones, Sangre de Cristo Range, *Brandegee s. n.* (MO). San Miguel Co.: Trout Lake, *Payson & Payson 4199* (GH, MO). Location unknown: Bear Creek, *Purpus 700* (F); Mirror Lake, *Clements & Clements 456* (C, GH, MO, NY, RM, US).

NEVADA: Esmeralda Co.: White Mts., *Duran 3105* (F, GH, JBM, MO, US).

NEW MEXICO: Santa Fe Co.: vic. Santa Fe, *Arsène & Benedict 16099* (F, US).

UTAH: Duchesne Co.: Mt. Emmons, *Hermann 5201* (GH, MO); Garfield Co.: Aquarius Plateau, *Dixon s. n.* (F), *Ward 623* (GH, MO, US). Summit Co.: Lamotte Peak, *Hermann 5973* (MO); lower Henry Fork Basin, *Maguire et al. 14451, 14619* (WS).

WYOMING: Albany Co.: Medicine Bow Mts., *Ownbey 176* (WS). Park Co.: Beartooth Mts., *Williams & Williams 3762* (GH, MO, NY). Sublette Co.: Wind River Mts., *Nuttall s. n.* (GH); Yellowstone Park, Lone Star, *Reynolds 74* (F).

The degree of variation in this species is quite as high as in the other species of the genus. While I have not seen the type of Thomas' *Gentiana glacialis*, I have seen a sheet from the Copenhagen collection labeled on the back in the lower left-hand corner, "*Gentiana glacialis*", and in the lower right-hand corner, "dedit Villars." This material is certainly authentic, and may even be an isotype. Villars, in his Flora, refers to Gmelin's 'Flora Sibirica': "Elle paroit gravée dans Gmelin Tab. 51. B. vol. IV. sous le nom de *gentiana pumila centaurii minoris folio flore piloso.* Stelleri pag. 105." This plate compares very closely with the Copenhagen specimen with the exception of the corolla, which is pictured as having five lobes. This feature is not critical, however, as such variation in lobe number is common throughout the genus with the exception of the fringed gentians where four parts are the rule. On the other hand, the five lobes may have been an error by the artist, for in all other respects the illustration is *G. tenella.*

Nelson described *Gentiana monantha* partially because he thought that the true *G. tenella* Rottb. was an arctic plant with 5-merous flowers: "The true *G. tenella* Rottb. is an arctic plant with 5-merous flowers, the obtuse corolla lobes as long as its tube; the calyx only half as long as the corolla and with unequal sepals." The original description of *G. tenella,* however, states: "fauce 4fida, barbata", and "Perianthium 4phyllum".

A small population from St. Paul Island, Pribilof Islands, Alaska, consists of rather short plants with a dense cluster of ascending branches. Both the 4- and 5-merous condition occurs and one or two calyx lobes are more broadly ovate than usual. This population may be referred to:

13b. Gentianella tenella (Rottb.) Börner, ssp. **pribilofii** J. M. Gillett, subspec. nov.

Plantae 3–5 (–8) cm. altae; folia caulinaria plerumque in rosula per contractionem internodiorum inferiorum; ramis numerosis ascendentibus. Flores (4)–5-meri; calycis lobis exterioribus tum 1 tum 2 latius ovatis.

ALASKA: Pribilof Islands: Seal Island, *Bryant s. n.* (US); St. Paul Island, *Elliott s. n.* (GH, US), *Kincaid s. n.* (CAN, C, NY); St. Paul Island, Behring Sea, in 1891, *J. M. Macoun* (CAN HOLOTYPE, GH, MO, NY), *in 1896* (CAN, US), *in 1892* (CAN, US), *in 1914* (CAN, GH, NY, US), *White s. n.* (GH, NY), *Whitney s. n.* (US).

Enumeration of the Species

Subgenus I. EUBLEPHIS

1. *G. detonsa* (Rottb.) G. Don
   - a. ssp. *detonsa*
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Vol. 44 NOVEMBER, 1957 No. 4

MORPHOLOGICAL COMPLEXES IN HOPS (*HUMULUS LUPULUS* L.) WITH SPECIAL REFERENCE TO THE AMERICAN RACE[1]

EDWARD L. DAVIS[2]

The genus *Humulus* cannot be treated taxonomically as can a plant known exclusively in the wild. Unlike many cultivated plants, hops are fairly easily established as escapes from cultivation, and the distinction between wild and cultivated hops is not easily drawn. One may be certain that the natural distribution of hops has been greatly modified by man. Yet hops cannot be studied only as cultivated plants if the origin and relations of the various cultivated varieties are to be understood. The record of hop varieties is so incomplete that the history of many of the most important cultivated varieties is not known with certainty. The relationships between these varieties, as well as the more fundamental and difficult question of the origin of cultivated hops, cannot be determined without a close examination of wild-growing hops. It has therefore been necessary to attempt a simultaneous study of cultivated and wild forms, though in the following paper the emphasis will be given only to the American hops. A later publication will consider the cultivated varieties of the world in more detail.

Hops have found many uses, in addition to that of flavoring beer, which have led to their cultivation over a wide geographical area. Sometimes the use has been such that hops have been cultivated in small gardens rather than in large fields. Many of the early medicinal uses were summarized by John Parkinson (1640) who noted that the young buds served "to open obstructions of liver and spleene, to clense the blood, to loosen the belly", and in clensing the blood hops help to cure "all manners of scabes, itch, ringwormes and spreading sores." Various parts of the plant were used: "seeds in powder taken in drink killeth the worm in the body; the juice of the leaves dropped into the ears clenseth the corrupt sores; a syrup, made of the juice and sugar cureth those that have the

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[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] University of Massachusetts, Amherst, Mass.

yellow jaundice, easeth headache that cometh of heate, and temper the heate both of the liver and stomach." Hops have found additional medicinal use in poultices for swellings and tumors, for relieving pain of gout and rheumatism, and for calming nervous irritation (Simmonds, 1877). They were widely regarded as having a soporific effect, and pillows were stuffed with them. This practice attracted attention when Dr. Willis, in 1787, prescribed the use of a hop pillow for George III (Johnson, 1867). Morgan (1952) suggested that the hop-screened front porches of rural homes in the northern part of the United States served to lull farm folks to sleep after a hard day's work. Dr. Edgar Anderson recalls the practice in upper New York State and Michigan during the nineteenth century of planting hop vines outside the bedroom window.

For these medicinal uses the quantity of hops required was not great, and sufficient was easily grown in the family garden. Such small scale, but widely practiced, cultivation has given man an unusually fine opportunity to alter drastically the natural distribution of this plant. According to De Candolle (1883), the hop is native to Europe and Asia, from England and Sweden as far south as the mountains of the Mediterranean basin, and in Asia as far as Damascus, the south of the Caspian Sea and eastern Siberia, and it is not native to India and China. Nuttall (1847) considered it certainly indigenous to western United States, but the following letter by Asa Gray[3] in answer to a request for American wild hops, does not give any suggestion that they are to be found in the East:

> There is hardly a doubt that all the hops raised in North America are originally from plants introduced from Europe. If these will answer the purpose, it would be easy to have a sufficient quantity of American-grown hops sent to London; still easier to obtain them in the London market. But if hops from the native *Humulus Lupulus* are desired, this will not be easy. They grow, indeed, in a scattered way along the banks of certain streams, from Canada west to New Mexico, probably also in Arizona, but, if there, certainly in the secluded mountains only, and being dioecious, they can only now and then be found in fruit. I have myself seen the plant growing wild, but never in such a way that I could have gathered a pound of dried hops.

There is morphological and cytological evidence, presented below, for the existence of an American race of hop, quite distinct, though in minor details, from the European hop.

Nomenclature

The genus *Humulus* has been placed variously in the families Moraceae,[4] the Urticaceae,[5] and the Cannabineae.[6] The question of the organization and size of families is beyond the scope of this treatment, and I am following Rendle[7] (1952) in considering it a member of the Cannabinaceae, with the closely allied hemp.

[3] In Am. Druggist 15:111. 1886.
[4] Engler, K., und Prantl, K. Nat. Pflanzenfam. III^1:96. 1888.
[5] Bentham, G., and Hooker, J. D. Genera Plantarum 3:356–357. 1883.
[6] De Candolle, A. Prodr. 16^1:28–31. 1869.
[7] Rendle, A. B. The classification of flowering plants 2:56–58. 1952.

Linnaeus, in the first edition of the 'Species Plantarum'[8] listed a single species *H. lupulus* L. Over one hundred years later, A. De Candolle, 1869, in his treatment of the Cannbineae, included three species in the genus: *H. lupulus* L., *H. cordifolius* Miq., and *H. japonicus* Sieb. & Zucc. He did, however, question the validity of *H. cordifolius* Miq.

H. lupulus and *H. japonicus* are very distinct species. The former is a perennial, with numerous lupulin glands upon the bracts and bracteoles of the cones, and the lower surface of the leaves, and with a diploid chromosome number of 20 (Ono, 1955, Sinoto, 1929, Winge, 1929). *H. japonicus* is an annual, with lupulin glands rare or absent, and a 2 N number of 17 in the male, 16 in the female (Kihara, 1929, Winge, 1929, Sinoto, 1929). *H. cordifolius* Miq. will be considered on a following page.

After 1753, the following names were used for the European hop in disregard of the prior Linnaean name:

Lupulus scandens Lam. Fl. Fr. 2:217. 1778.
L. communis Gaertn. Fruct. 1:358. *t. 75.* 1788.
L. amarus Gilib. Exercit. 2:451. 1792.
H. volubilis Salisb. Prod. 176. 1796.
H. vulgaris Gilib. Hist. Pl. Europ. 2:343. 1798.
H. aculeatus Nutt. in Jour. Acad. Philad. N. S. 1:182. 1847.

Nuttall (1847) considered that the hop native to western United States was distinct from the European *H. lupulus.* He established *H. americanus* from a collection made by Dr. Gambel in New Mexico. His description and comments follow:

> *H. americanus:* Leaves 3 to 5 lobed, the upper sometimes entire, inner divisions lanceolate-acuminate, denticulate along the apex; scales of the cone ovate, acute, the lower ones acuminate.
> I have ventured, as I think, upon sufficient grounds, to separate the American from the European hop, found as it is in the uncultivated interior of the continent beyond the reach of inhabitants, our plants must necessarily be indigenous. I have compared the present with the foreign plant with some attention, and I can in all cases readily distinguish them by their foliage. In the American plant, whatever be the other variations of the leaf, the attenuated points are denticulated nearly to the extremity. In the European the summit of the leaf is abruptly toothed. In the native plant, the male flowers appear to be smaller, and the scales of the cone are likewise acuminate. In some specimens, as in the European plant, the upper leaves are simply cordate, and entire, but in all cases the denticulations are smaller, and more numerous.

This separation was not universally accepted, and Asa Gray retained but the single species *H. lupulus* L. in the revised edition of his 'Manual'.[9] Still later, other attempts were made to establish an American segregate. Nelson and Cockerell[10] proposed the variety *H. lupulus* L. var. *neomexicanus.* Again the type was from the Southwest (Beulah, New Mexico). The lateness of the date should not pass

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[8] Sp. Pl. p. 1028. 1753.
[9] Man. Bot. North. U. S. p. 400. 1857.
[10] Proc. Biol. Soc. Wash. 16:45. 1903.

unnoticed. In the fifty years since Nuttall's collection there was much opportunity for cultivated forms to become established as escapes.

There is absolutely nothing in their descriptions which would make it possible to differentiate between the American variety and *H. lupulus* L. of Europe, except the geographical location. The acuminate fruiting bract used to set off the variety occurs widely among European hops, both wild and cultivated.

Rydberg, in the 'Flora of Colorado',[11] lists the single species *H. lupulus* L. *neomexicanus* Cockerell for the Rocky Mountains. He says: "The native hops of the Rocky Mountain region has deeper divided leaves and more sharply acuminate bracts than the cultivated variety. It grows along streams from Wyo. to Utah, N. M. and Ariz."

This represents the first suggestion that the American type may be identified by the divisions of the leaf. By 1917, Rydberg had raised the variety to the species level.[12] The lobing of the leaves in the inflorescence, which he used in the key, is highly variable and not of any taxonomic significance.

At best, the descriptions and keys of the above authors permit the classification of some herbarium specimens into one or another species or variety. They do not establish a type found predominately in North America and separated from all European forms. The confusion is summarized by Fernald[13]: "The native plant sometimes called *H. americanus* Nutt., *H. lupulus* var. *neomexicanus* Nels. & Cockerell and *H. neomexicanus* (Nels. & Cockerell) Rydb.; its characters evasive."

Extensive comparisons of European and American hops bring out, above all, their great similarity. It is possible to differentiate between the European and American type on the basis of a complex of characters, but only when cone and leaf material is carefully collected. Consequently, I consider that for the present it is advisable to retain the name *H. lupulus* L. for the wild perennial hop of Europe and America.

The annual *H. japonicus* Sieb. & Zucc.[14] is a very distinct species which, because of the small number of lupulin glands, has never been used in the making of beer. Native to Asia, it is now widely scattered in North America as an adventive weed. Merrill[15] proposed using the name *H. scandens* (Lour.) Merr. for *H. japonicus* on the following grounds:

> Loureiro's poor description [of *Antidesma scandens* Lour. 1790], based upon a nearly glabrous form for which he saw only staminate specimens, applies unmistakably to the species currently known as *H. japonicus* Sieb. & Zucc. No other known Kwangtung species in any family remotely conforms to the characters indicated by Loureiro.

Loureiro's description is extremely vague, and I am following Fernald in retaining *H. japonicus* Sieb. & Zucc.

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[11] Fl. Colo. p. 100. 1906.
[12] Fl. Rocky Mts. & Adj. Plains, p. 408. 1917.
[13] Gray's Man. Bot. p. 556. 8th ed. by M. L. Fernald. 1950.
[14] Fl. Jap. Fam. Nat. 2:89 (Abh. K. Akad. Münch. math.-nat. Kl. 4^2:213. 1846.
[15] Merrill, E. D. A commentary on Loureiro's "Flora Cochinchinensis." Trans. Amer. Phil. Soc. n. s. 24^2:138. 1935.

Maximowicz[16] makes reference to his reduction of *Humulus cordifolius* Miq. to a variety, noting that De Candolle had erred in placing it near *H. japonicus* in his key on the grounds that lupulin glands were absent on the bracts and bracteoles. On the contrary, Maximowicz emphasizes the presence of such glands by concluding that it is as suitable for use in brewing as is the European hop. Miquel's description[17] is very incomplete, being based only upon female material, and Maximowicz did not clarify the situation. Hance[18] provided the first description of the male plant, but the description contains nothing which could be used to separate it from *H. lupulus*. Furthermore, an examination of specimens from Maximowicz's collection shows it to be identical with the European hop. Consequently the names *H. cordifolius* Miq. and *H. lupulus* L. var. *cordifolius* Maxim. are placed in synonymy with *H. lupulus* L.

Morphology

Until recently only brief accounts of hop morphology had been published despite very extensive studies conducted upon certain parts of the plant. Within the last two years, however, this situation has radically changed. Ehara (1955) has made a comparative study of *H. japonicus* Sieb. & Zucc. and *H. lupulus* L., including anatomical observations as well as descriptive comparisons starting from the seedling stage. Hamaguchi (1955) published an even more extensive work on *H. lupulus* L. including developmental analysis of the vegetative and flowering shoot. As a consequence of these publications, a detailed account of the morphology of the hop plant will not be presented here, though a description of the inflorescence of the female plant is required for the discussion which follows. Unless otherwise indicated, all observations apply to *H. lupulus* L.

The small pistillate flowers, each consisting of a cup-like perianth and a single pistil with two elongate stigmas, are borne in the axils of bracts and bracteoles upon a condensed axis, forming the cone. Multicellular glands, containing lupulin, are found in great number upon the bracts and bracteoles.

The cone itself is a greatly condensed inflorescence, readily differentiable into nodes and internodes. At each node are normally found four flowers. This node is really a complex structure best understood from fig. 1 (modified after Hamaguchi, 1955, p. 94) in which three are diagrammed. The internodes a^1 and a^2 are reduced to the point where they are barely visible, thus condensing two nodes of these secondary axes back upon each node of the primary axis.

The nodal cluster has been interpreted as cymose, with the median flowers abortive (fig. 2). When all bracts and bracteoles are removed, the cone appears in side view as shown in fig. 3A. Each nodal cluster then appears to be subtended by a single bract scar. When turned through 90°, however, it is seen that two

[16] In Franchet & Savatier's Enum. Pl. Jap. 2:489. 1879.
[17] Ann. Mus. Bot. Lugd. Bat. 2:133. 1865.
[18] Jour. Bot. (Brit. & For.) 20:293–294. 1882.

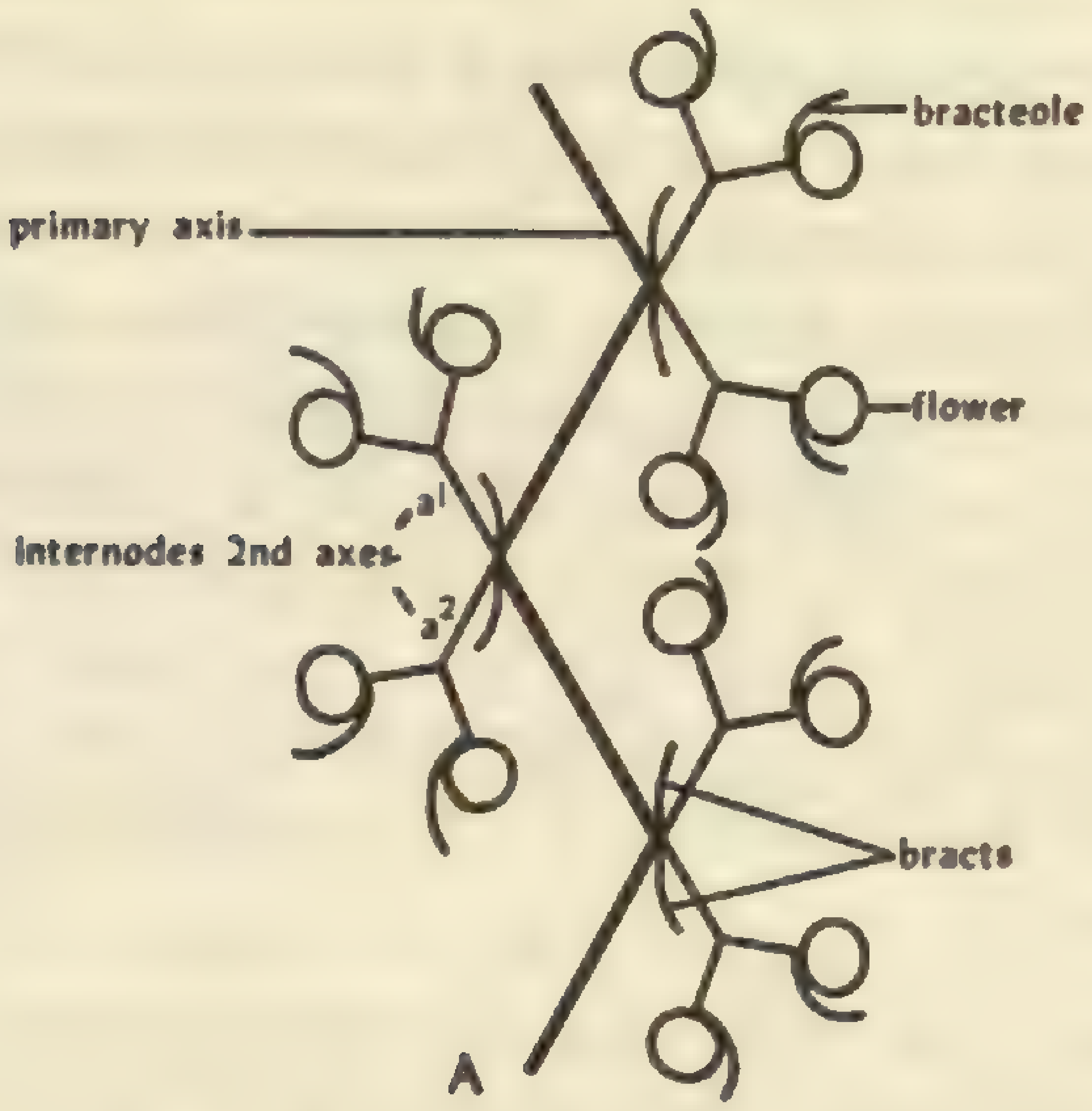

Fig. 1. Diagram of a hop cone showing three nodes. Internodes of secondary axis are much enlarged.

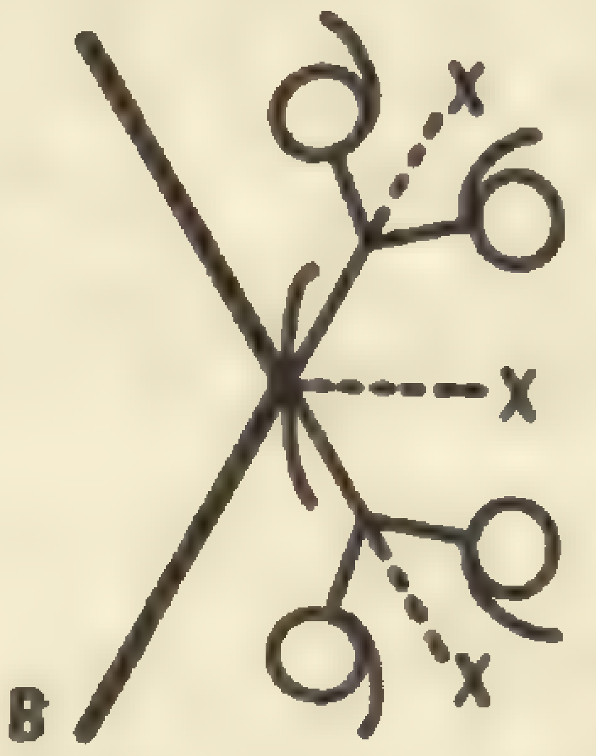

Fig. 2. A cluster of flowers at a single node of cone. Abortive flowers indicated by X.

scars occur at the base of each cluster of four flowers (fig. 3B). Rendle[19] has interpreted these as stipules of a former bract. Though the two scars are not usually inserted at the same level, one appearing slightly above and overlapping the other, the infrequent cone with well-developed foliage leaves confirms Rendle's interpretation. In such cases the petiole is found directly between the two scars, which are at the same level (fig. 3C). The slight displacement found in the normal cone must be attributed to a secondary effect of growth. Moreover, these stipular bracts (which are so widely known in the hop literature simply as bracts that they will be so called henceforth) show a vein pattern similar to that of the stipules throughout the vegetative parts of the plant, while being very different from that of the bracteoles.

Material

Much of the analysis of hops throughout this study has been based upon cones. They contain many diagnostic characters and are readily obtainable from many parts of the world. Some of the cones used for analyses were small samples taken from the pressed bales which are submitted to brewers for their evaluation of the crop. Though the cone material itself is not inferior to field collections, it is of course not possible to determine the number of plants represented in any such sample. The elaborate method of machine picking so thoroughly mixes up cone material that as an approximation each cone may be considered to represent a different plant. In addition to the brewers' samples, cones and leaf collections have been made in the field. With these, though each cone is selected from a different plant, the number of clones represented may be small.

[19] Classif. Fl. Pl. 2:56–58. 1952.

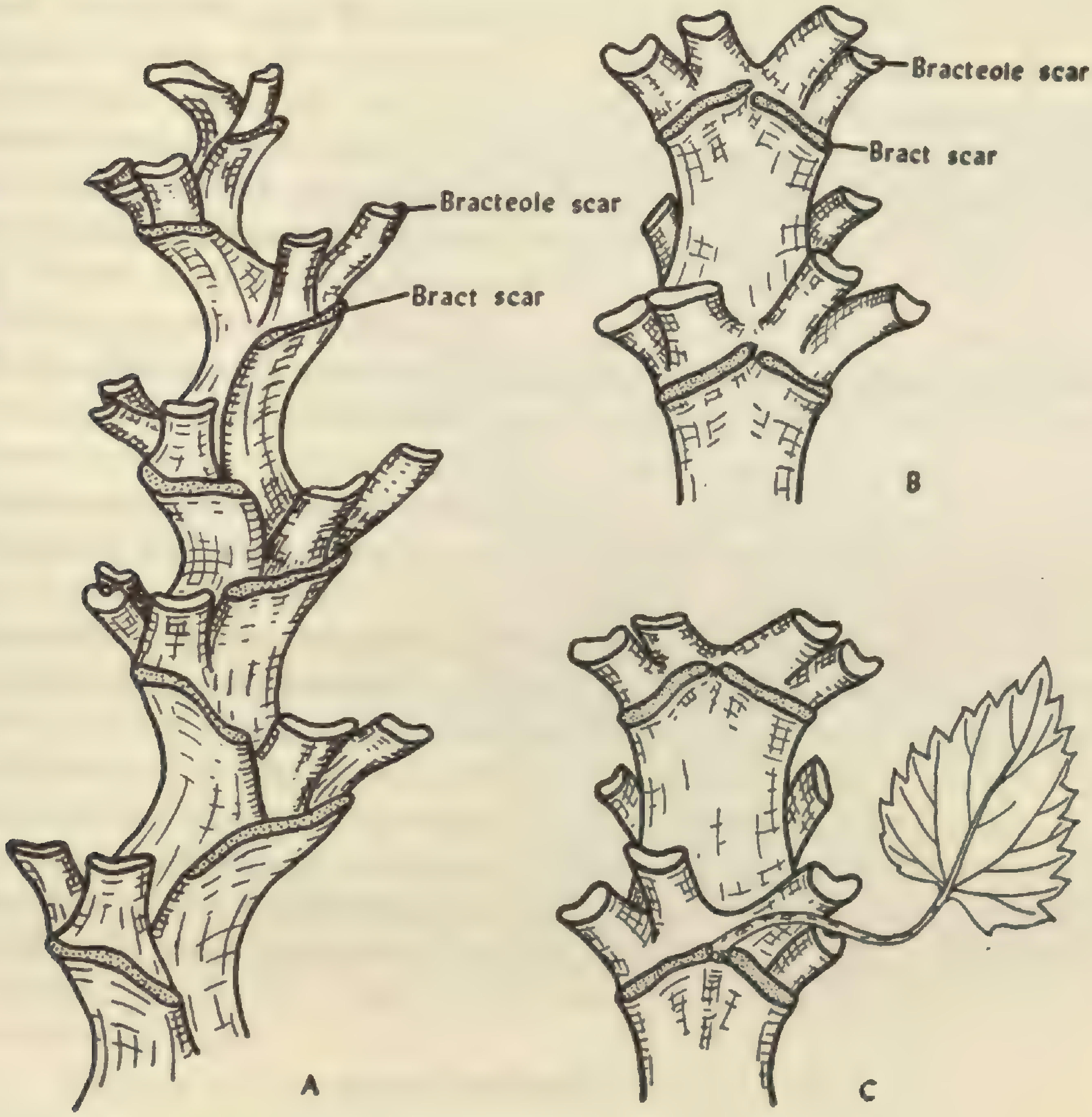

Fig. 3. Hop cone axis with bracts and bracteoles removed: A, resting on flat surface; B and C, turned on edge; C, abnormal cone bearing foliage leaf.

Some knowledge of field practices is imperative for an understanding of the field samples. Ideally, every hop field of the same variety belongs to the same clone. Vegetative reproduction, by cuttings, is the only method used commercially. Each spring, or for the sake of economy every several years, soil is dug back from the hop hill and all but a few of the young shoots are cut off. The cut shoots are then used to replant old hills, or for new plantings. It is a standard procedure for farmers to sell excess hop roots to neighboring farmers, or at the present time, in the large organizations of growers, to ship roots from state to state. Only rarely, when new fields are being established, will such additions be kept separate. More generally new plantings are intermixed with old. This, by itself, would not offer complications if each variety remained true to type. However, not only have some new varieties been attributed to bud sports, but innumerable worthless rogues occur each year. The superintendent of one farm in California reported he was removing almost 20 per cent of the hills because they

were off type. This was after many years without roguing, but several farmers have suggested that about 5 per cent of the plants each year are rogues. To my knowledge, no research has been done upon the source of such rogues. They may represent vegetative mutations, seedlings, or carelessly introduced contaminants.

The tale told by an Oregon farmer (though it may be an unusual case and somewhat exaggerated) illustrates how contaminants may be introduced during replanting fields. He had purchased roots which he believed to be of a single variety of hop. After planting them on his own farm two-thirds of them grew into willow trees! The sequence of events which led to this can easily be followed. In many areas, the spring root cutting is not done under the surveillance of the superintendent, but the field is let out to a cutter who receives as pay the root cuttings he makes. The temptation to add to the yield by collecting roots of escaped hops from the roadsides is occasionally too great. To the contamination from such weed hops had been added the frequently present willow whose shoots are readily confused with those of hops.

Besides the over-all sampling problem which results from the field heterogeneity is the heterogeneity of the individual hop hill. Almost without exception more than one root is planted per hill; most frequently the number is three. In making the collections of leaves and cones I attempted always to take both from the same vine. Usually the effort was successful. However, since four (or more) vines are trained to each wire, and these vines may originate from different root stocks, it was necessary to trace the cone-bearing side branches back to the main vine at the level (5 or 6 feet above ground) at which leaves had been selected. This always introduced opportunity for error.

Varietal Identification

Before turning to the morphological characters which have been used here, some previous efforts to describe varieties on structural characteristics will be considered. In the description of new varieties, it has been a standard practice to make use of cone shape, size, and coloration. Such descriptions are of obvious use to the grower, at least in so far as they are not too generalized. Unfortunately, exactness is not easily attained. Moreover, cone shape and size are greatly influenced by pollination. For instance, a variety such as LATE CLUSTERS, which produces long cones with prominent dark green streaks (the bracts) alternating with light green streaks (the bracteoles) when unpollinated, regularly has nearly spherical cones, without streaks, after pollination. Although this type of varietal description is useful to growers familiar with these changes, it is not suitable for describing pressed material, nor is it of great value to the botanist or geneticist. It is only when more definitive characters are used that it will be possible to trace the inheritance patterns in hops.

Beyond studying the varietal descriptions, many efforts have been made to study other morphological features of hops. Only a few need be mentioned here. Wormald (1915) undertook an extensive examination of male hops. Leaf color,

texture, lobing, dimension of lobes, gland number and distribution were scored. Salmon and Wormald (1921) studied time of flowering, color of stem, relative number of glands on the leaves, and on the cone; size, shape, aroma, and color of the cone axis. Schmidt (1918) investigated the possibility of characterizing clones by the number of marginal teeth on the leaves. This investigation, carried out over a number of years, provided valuable information on the change in leaf shape which takes place as a plant becomes established. More recently, Meneret et al. (1954) have reported on the use of the length-width ratios of bracts as a means for varietal identification.

In the present study six characters have been chosen for scoring. They represent various modifications of the characters previously used. Even more important is the semi-graphic method of expressing the results (Anderson, 1949). By this means it is possible to identify a hop sample by plotting it out and comparing it with previous plottings of known varieties. The advantage is not only in its usefulness in identifying varieties, but also in that genetical relationships are suggested when suitable botanical characters have been selected for scoring. Identification of hop varieties is not the primary concern of this paper. Rather attention is being focused upon the morphological complexes within *H. lupulus.* Evidence suggests that these complexes, which are based entirely upon structural features, correspond to certain chemical and perhaps cytological groupings within the species. If additional research confirms this, such morphological features as are used here will have an increased value in hop breeding. At the same time it will provide an interesting example of the use of chemical, morphological, and cytological evidence for the establishment of taxa below the level of species, where morphological evidence is not adequate by itself.

The following six characters have been scored and the results expressed in pictorialized scatter diagrams: On the leaf: (1) dentation number, (2) pubescence type. On the cone axis: (3) condensation; (4) angularity; (5) bract scar type. On the bract: (6) number of main veins extending into the terminal third.

LEAF:

(1) *Dentation.*—The leaf shape, and consequently the dentation number, is exceedingly variable upon each hop plant. To attempt to describe plants upon the basis of a few randomly selected leaves would be impossible; merely increasing the number of leaves sampled has not proved very satisfactory. Leaves found at the lowermost nodes are distinctly different from those at higher nodes and in the inflorescence. The leaves of the secondary and tertiary axes differ from those of the primary. Despite this great variation, truly homologous leaves may be obtained by making the selection from a main vine (one of the vines trained up from the hill) of a mature plant. In this way, the phenotypic variability can be reduced to measurable proportions. The leaves in all field collections have been taken from the main vine, at a height of about five or six feet. The dentation count was made on the median lobe of the leaf in the following manner: From the number of all

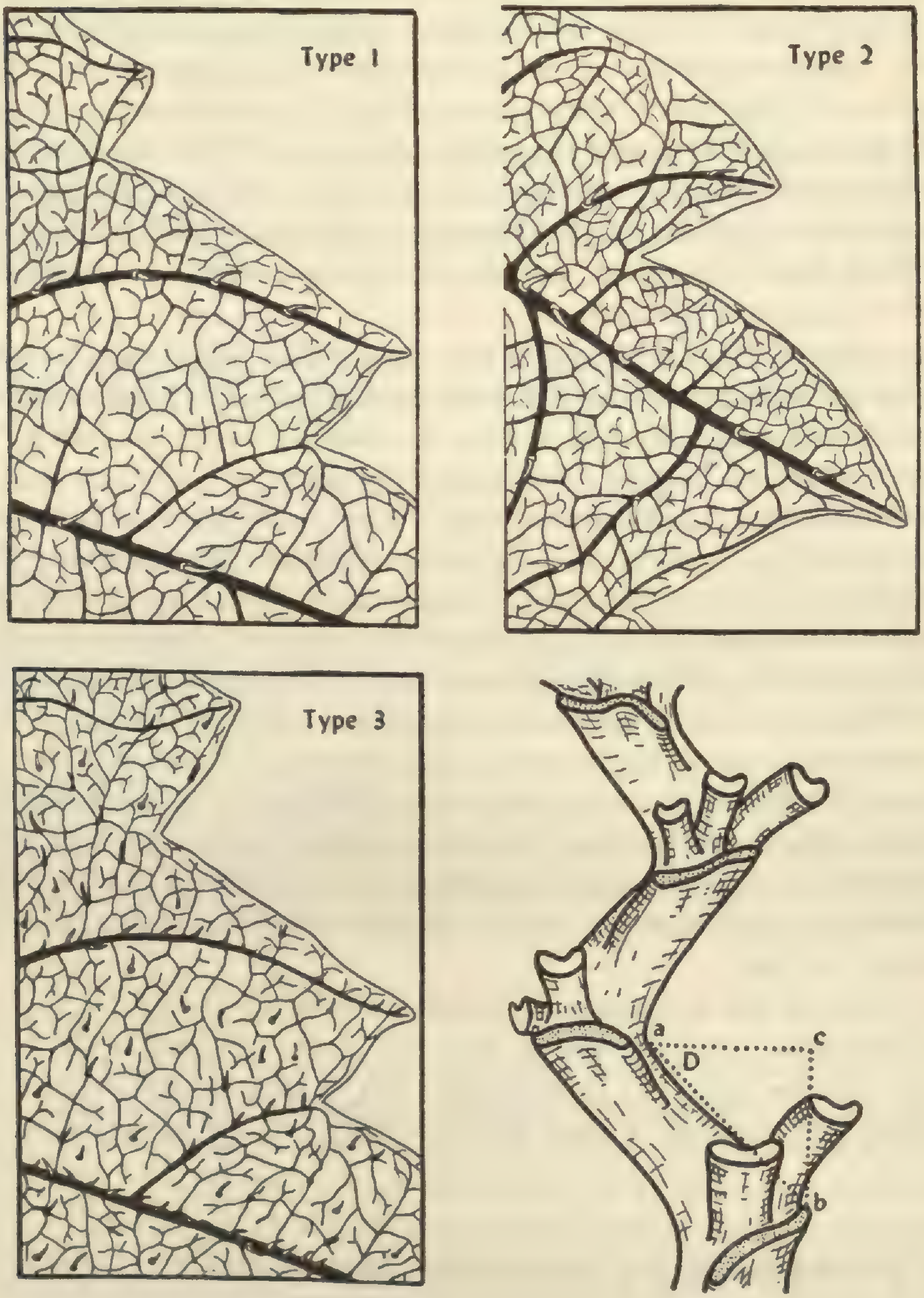

Fig. 4. Under surface of hop leaf drawn at margin, showing three different pubescence patterns. Lower right, showing method of measuring angularity.

dentations counted, was subtracted the number which were not provided with a distinct vein visible to the unaided eye, the result giving the "major dentations". The number of minor dentations was also recorded in each case, but was so variable within every variety that it did not contribute to their identification and has been eliminated. In addition, the number of dentations within 5 cm. from a point on the edge of the lobe to the last dentation at the lobe apex was counted.

Since Schmidt's work (1918) had shown that dentation number steadily in-

creased during the first three years that a plant is becoming established, collections were made only from plants four years or more old, unless otherwise indicated.

(2) *Pubescence.*—The number of hairs per unit area upon the under side of the leaf undergoes tremendous variation, and is not by itself a satisfactory character. Of greater importance than the number is the pattern of their distribution. Upon all hop leaves, hairs are found on large veins. Type 1 was made up of leaves with hairs on major veins only; type 2 with hairs upon these and upon secondary veins as well; type 3 was characterized by the presence of hairs upon all veins, down to those of the smallest, and between veins on the vein islands. These types are shown in fig. 4. In most cases, type 3 possessed the most hairs in an absolute sense, but when the leaves approached the glabrous condition, hairs were not confined to large veins, as in the nearly glabrous leaves of type 1. With but few exceptions known clones remain constant as to type.

CONE:

(3) *Condensation of the axis.*—Using a dissecting scope, the length to the nearest mm. was measured between five bract scars. These were taken at the base of the cone, or at least never including the two uppermost nodes.

It is to be expected that the greatest disturbing influence upon this and the following character is pollination. Since pollination is known to produce profound changes in the cone axis, only unpollinated (seedless) cones are compared, unless otherwise indicated.

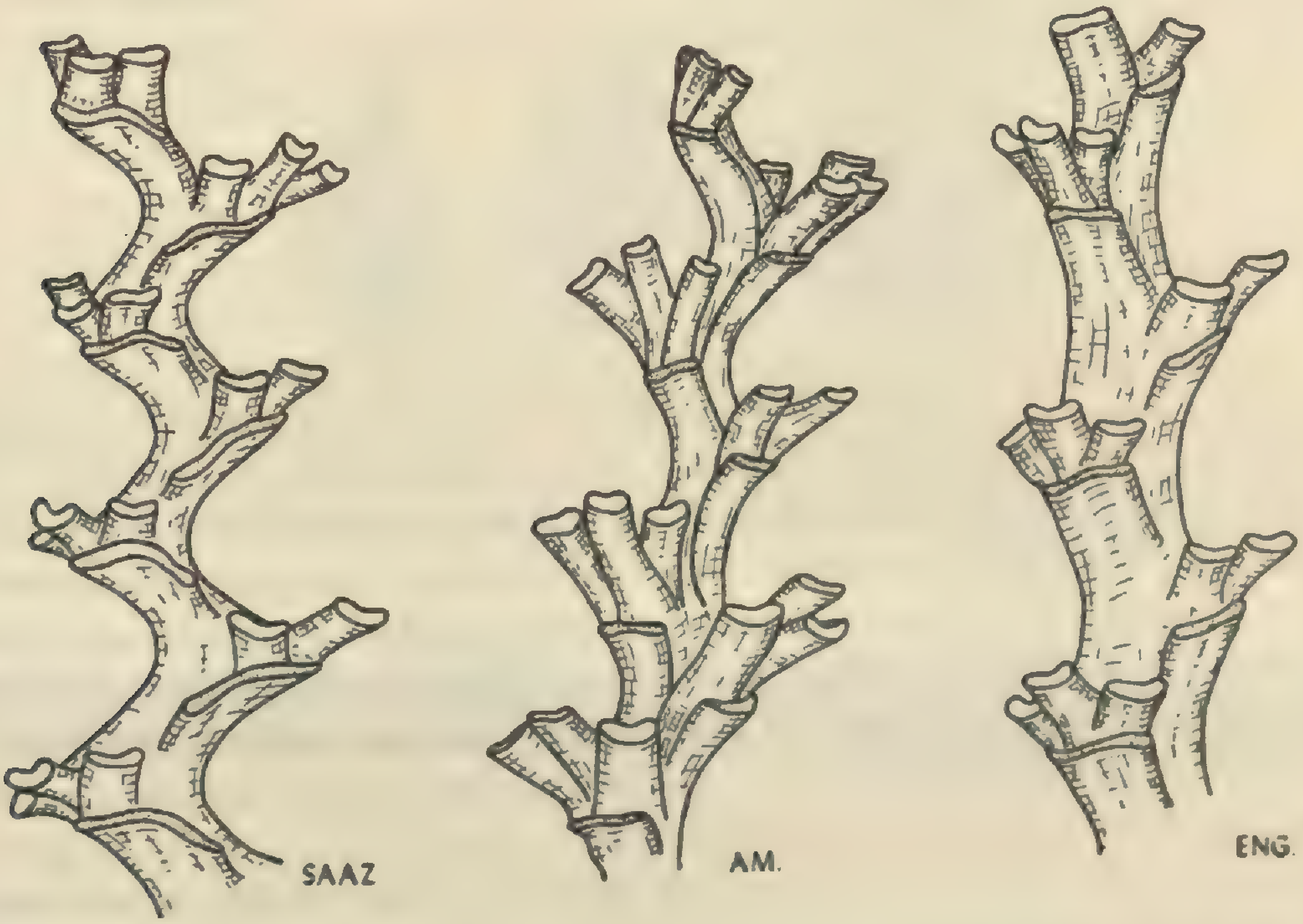

Fig. 5. Cone axis of three different varieties: SAAZ, Czechoslovakia; AM, LATE CLUSTERS; ENG, FUGGLES.

(4) *Angularity of the axis.*—The angularity of the axis was measured with the use of an eye-piece micrometer and dissecting scope. A line *ab* (fig. 4) was drawn with the micrometer parallel to the axis, and then lines *ac* and *bc* were measured; from the right-angle triangle so constructed, angle *D* was obtained. This angle was in turn doubled, thus giving an approximation of the angle naturally formed.

(5) *Bract scar.*—The scar left by removal of the bract, when seen in side view, is classified as either elongated (stretching nearly between nodes of the axis, fig. 5 SAAZ) or abbreviated (confined to the area immediately below the subtended fruits, fig. 5 ENG.).

The type of bract scar served to make a major division between varieties. The scar is definitely independent of the degree of condensation or angularity of the axis as is shown by the retention of form without regard to the changes produced by pollination.

BRACT:

(6) *Vein number.*—Brewmasters have long realized that different varieties have different-shaped bracts. Such differences may be of considerable value though the variation within a cone, from base to tip, is great. Meneret et al. (1954) have been determining length-width ratios over a period of years. Though their report is optimistic, they concluded that this measure was "not completely definitive and should be considered along with other characteristics in identifying the type." Here, the same problem was approached in another fashion: the number of major

Fig. 6. Three principal bract types.

veins extending into the terminal third of a bract was recorded. This is itself correlated with shape, a low count being found on the long acuminate bract, a high one on the obtuse bract. For the present it appears to be more satisfactory than shape, at least for establishing differences between complexes. However, a more specific measure is necessary if individual varieties are to be differentiated. In order to establish uniformity for the measurement used, one of the first three bracts at the base of the cone was chosen each time.

When scored in this manner, the vein number for any variety is not constant. The range varies with the variety, but even with this variation, the populations fall into groups 7–8, 9, 10 or more. Fig. 6 shows a bract of each type.

Varietal Stability

Among the most discussed, but least exactingly studied, characteristics of hops, is their reputed ability to adapt to each new environment and assume the qualities attributed to that particular region. Such views are still widely found among growers. One of the popularly held examples of this "adaptation" is based on the effect of pollination upon cone shape and color as mentioned above. LATE CLUSTERS produces long cones with dark green and light green stripes when grown in California, Washington, and Idaho. Those in Oregon have more nearly spherical cones without striping. The essential difference between these types is not in the area in which they are grown, but in the presence or absence of seeds. The Oregon area hops, which are always seeded, have a characteristic cone, as do the uniformly seedless California forms.

In the selection of the foregoing tools of analysis, a strong emphasis was placed upon the stability within a clone as a measure of reliability. That fact at once prejudices their use in the evaluation of the uniformity or variability as it exists within each variety over time and space. A comparison of LATE CLUSTERS from California, Washington, and Idaho, for the year 1955 (figs. 7 and 8) shows how little the difference is, in these morphological characteristics at least, within that geographical range. The variation is not significantly greater than the individual plant variation shown in fig. 9, in which the leaf and cone measurements have been arbitrarily combined.

Another comparison is based upon leaf scores only. Fig. 10 shows leaf lobe number and dentation scores for LATE CLUSTERS. For the populations studied, the leaf lobe number was greater in Idaho (median 7) than in California or Washington (both with median 5). The dentation number is also greater in Idaho (42) than California (38) or Washington (36). That this may be attributed to larger leaves in the well-irrigated fields of Idaho is indicated by the dentation count per 5 cm. of leaf margins, both California and Idaho having a median of 12 and Washington a median of 11.

The constancy in the morphological characters measured here in different geographical areas speaks well for varietal consistency. The number of morphological characters which may undergo some change of course is not known, but they are certainly not of enough magnitude to warrant a fear of varietal instability. It must be recognized that genetically based characters may be such that they will remain virtually unchanged over the area within which the plants may grow, or they may be capable of a fluctuating expression under changing conditions. In the latter case, they are no less genetic.

Explanation of Symbols Used in Scatter Diagrams (Figs. 7–9, 12–14)

Number of main veins at tip of lower sterile bract:

7-8
9
10-11

Pubescence:

Hairs on main vein only

Hairs on main and minor veins

Hairs on and between veins

Number of teeth on median lobe of leaf:

20-26
27-33
34-+

Bract scar:

Elongated

Abbreviated

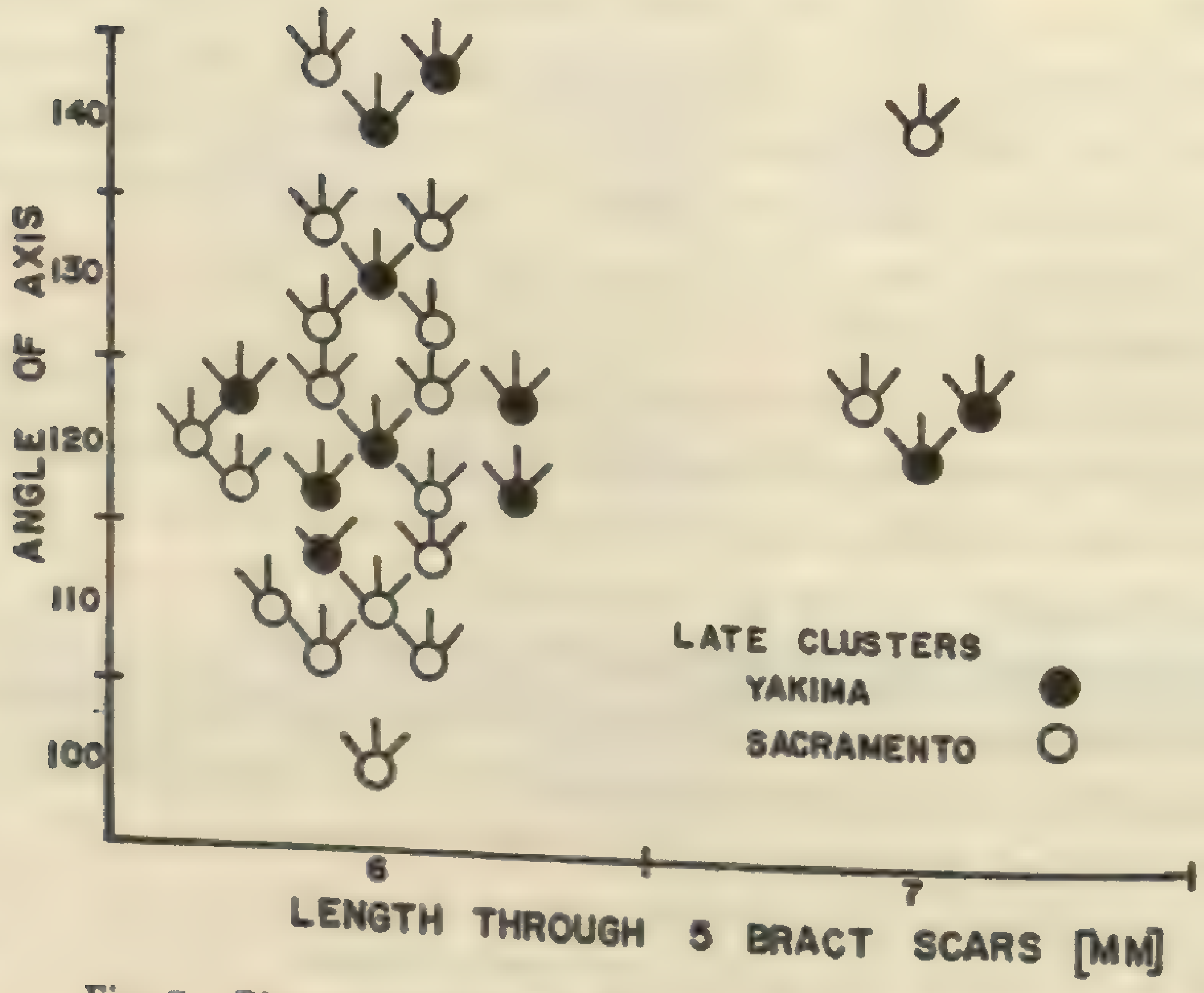

Fig. 7. Pictorialized scatter diagram of LATE CLUSTERS from Washington and California.

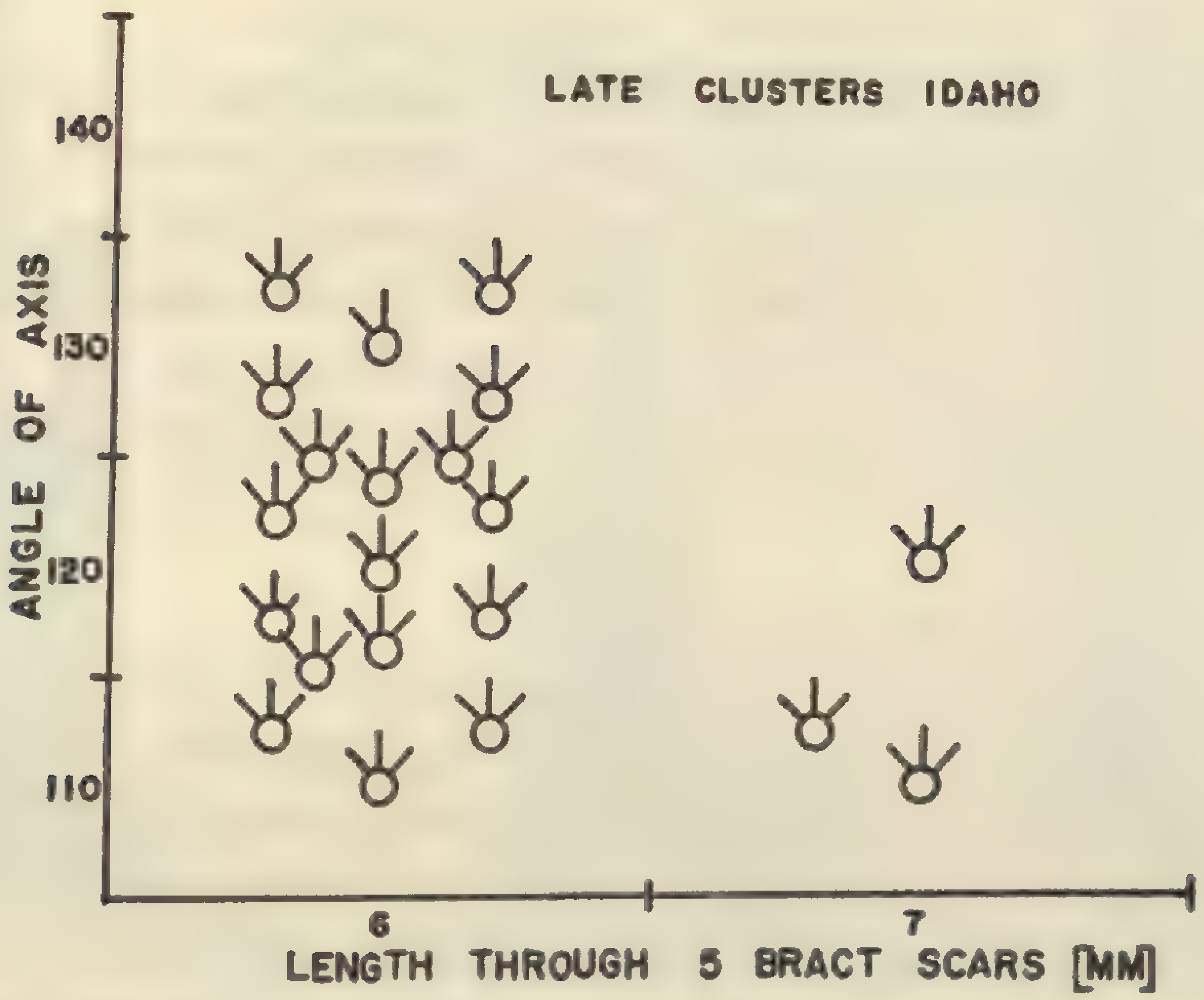

Fig. 8. Pictorialized scatter diagram of LATE CLUSTERS from Idaho.

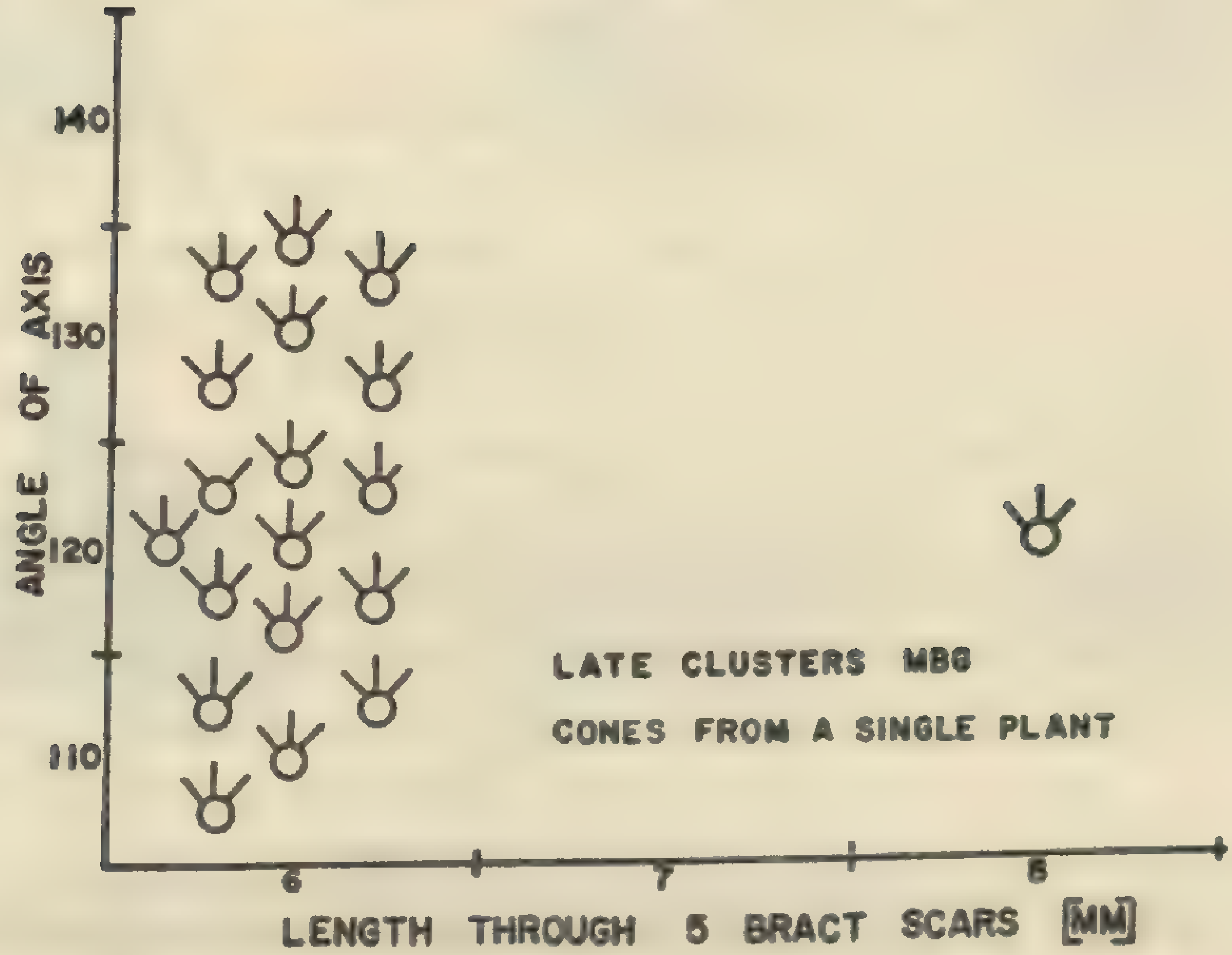

Fig. 9. Pictorialized scatter diagram of LATE CLUSTERS, leaves and cone taken from a single plant.

Distribution of Varieties within Morphological Complexes

The lobe and dentation scores for LATE CLUSTERS and FUGGLES, BREWER'S GOLD, BACKA, and HALLERTAU are presented in figs. 10 and 11.

Pictorialized scatter diagrams based upon populations of FUGGLES, BREWER'S GOLD, BACKA, and HALLERTAU hops have been presented elsewhere (Davis, 1956). It is sufficient here to consider composite scatter diagrams which have been plotted for these and other varieties using mean values for the axis measurements and median arm scores. One of these is based upon field samples (fig. 12) and is therefore scored for all characters. The other is based upon brewing samples (fig. 13) and does not show leaf scores.

Interpretation of results.—

Though the leaves of FUGGLES, BACKA, and LATE CLUSTERS all have median lobe numbers of 5, there are marked differences in the populations. FUGGLES and BACKA hops, not known to have any American relationship, have virtually no leaves with more than 5 lobes, and are outstanding in their uniformity. Seven-lobed leaves are frequent on plants of the American LATE CLUSTERS, and up to 10 lobes may occur. BREWER'S GOLD, an English variety with a female "wild" parent from Canada, has even a larger proportion of 7-lobed leaves, though the maximum is again 10. While large collections will show these differences strikingly, and it seems reasonable to attribute differences in potentiality to these varieties, individual plants can not be identified by this leaf character because of the great overlap between varieties.

In total dentation number, the European varieties are low, and distinctly separate from the American LATE CLUSTERS.

The scatter diagrams of the individual populations of LATE CLUSTERS (figs. 7 and 8) are more variable than the collection from a single plant (fig. 9). Though this suggests that every member within the population may not be of the same clonal origin, the variation is minor compared to that occurring in the Oregon field (fig. 14) in which off-types were known to be growing.

A study of the composite scatter diagrams (figs. 12 and 13) suggests that cultivated hops fall into three complexes: One, with a much-condensed very angular axis; a second with an elongate, straight axis; and a third, somewhat between the two in axis characters, but extreme in leaf and bract characters. Considering the history and region of cultivation of the varieties composing these complexes, the complexes are seen to consist of hops from (1) Germany, Czechoslovakia, Yugoslavia, (2) England, and (3) the United States.

Bringing together the cone axis, pubescence, dentation and lobing measurements, the three morphological complexes may be described as follows:

(1) *Continental complex:* Cones with condensed axis, markedly zig-zag; bract with 8 veins extending into the terminal third; elongated bract scar, reaching between nodes of axis; leaves with low number of dentations and lobes. On the undersurface of the leaf, hairs on major and minor veins but not between veins

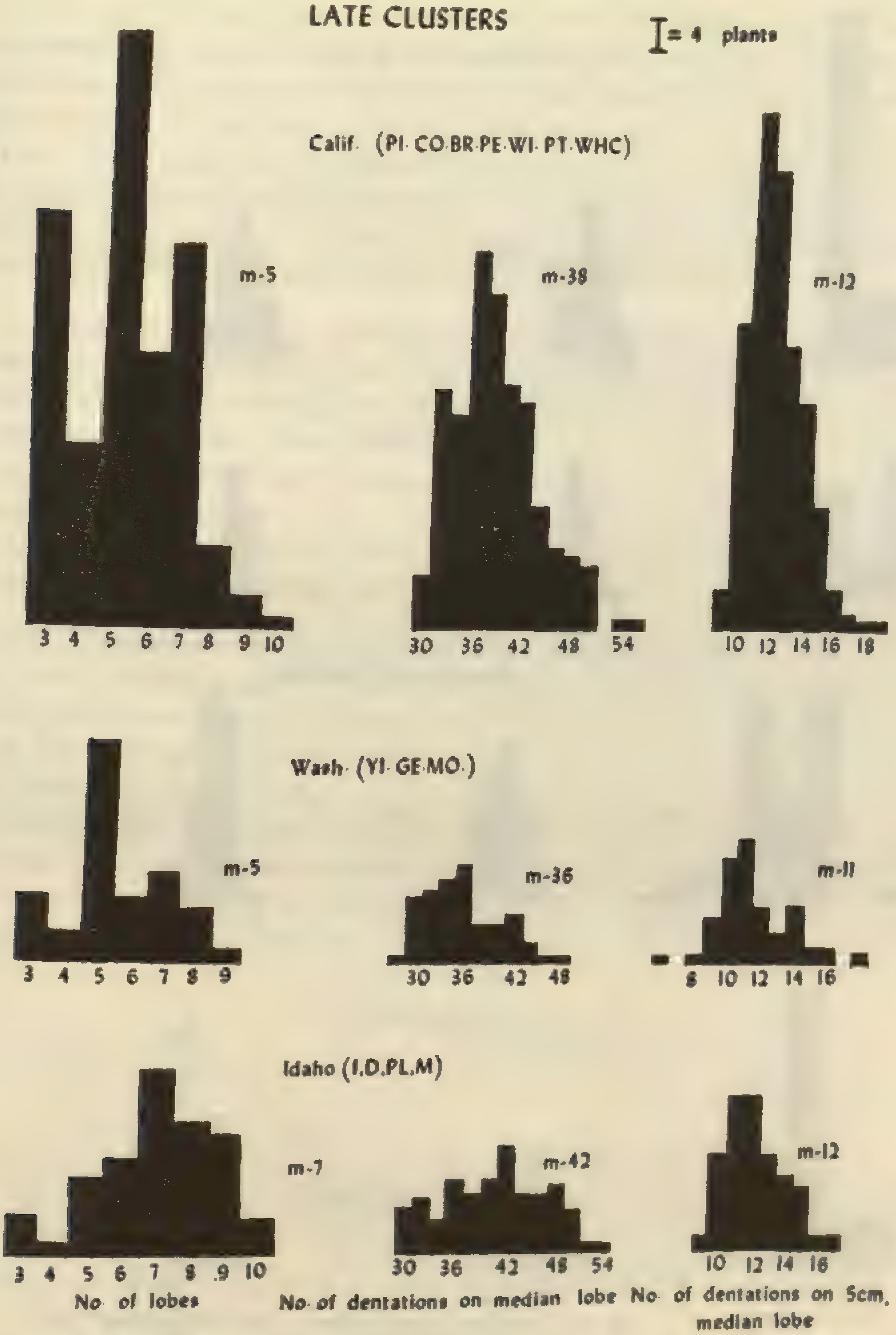

Fig. 10. Scores of leaf lobe and dentation number for LATE CLUSTERS from California, Washington, and Idaho.

(type 2). Though only a single variety (HALLERTAU) of this complex has been studied extensively for pubescence, the uniformity in cone structure throughout the group suggests that the leaves may be very similar also. This is given some additional support from the types of pubescence found on European herbarium

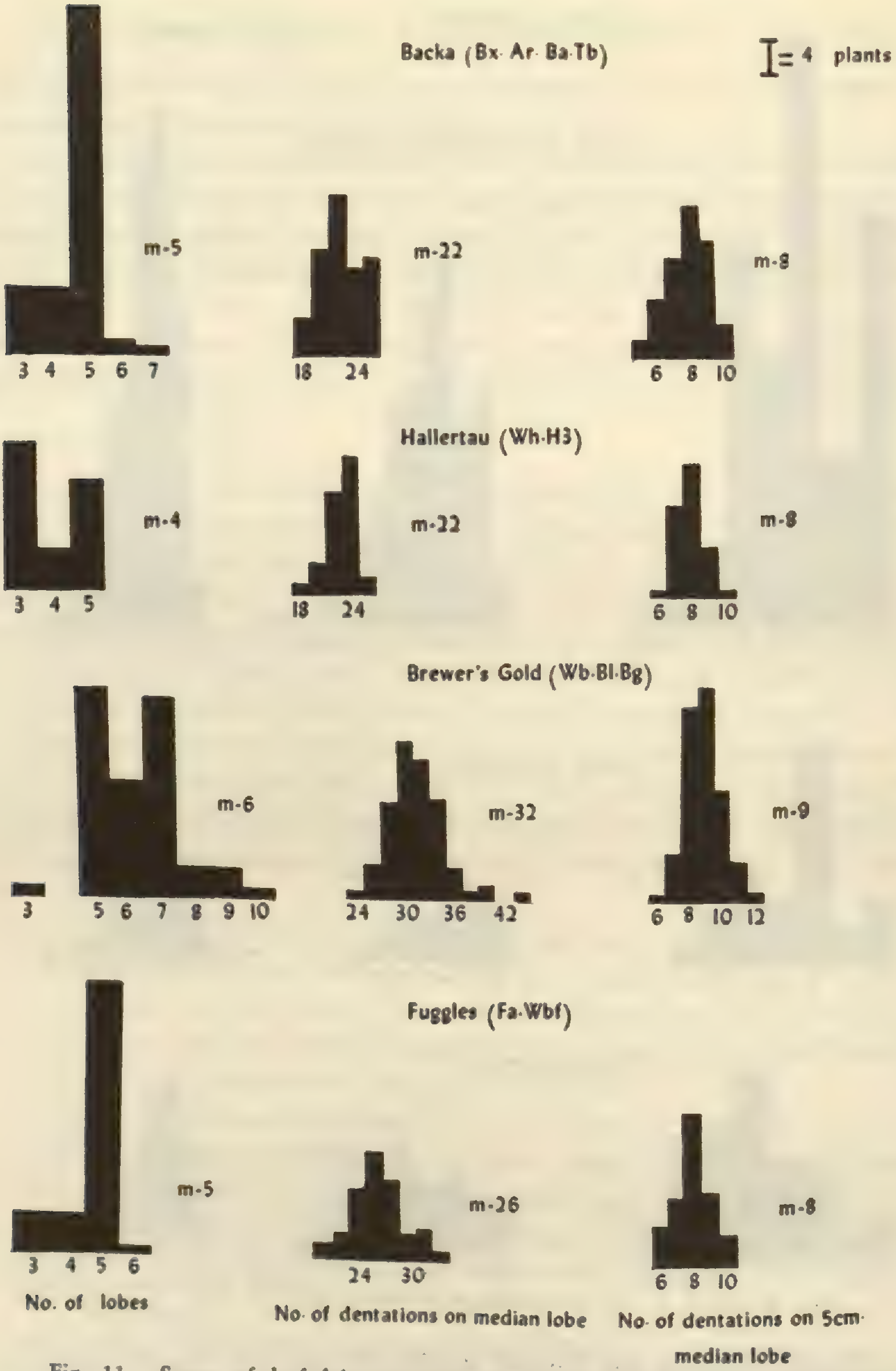

Fig. 11. Scores of leaf lobe and dentation number for BACKA, HALLERTAU, BREWER'S GOLD, and FUGGLES.

specimens of reputedly wild growing hops. A representative cone axis is shown in fig. 5 (SAAZ).

At the present, within the complex of continental hops it is possible to establish a gradation, starting with HALLERTAU and SAAZ, and running through TETTNANG

to BACKA and STYRIAN hops. It is not yet possible to identify every variety positively due to the limitations of the material available for study. Brewing samples of continental hops may not always be of a single type, but of two or more closely related types. The replacement of cultivated varieties in the field is often gradual and not always complete. When closely related types are in the same sample, whatever variation occurs must be considered as representing the natural limits of variability of that variety. As more characters are added to the complex, it will become possible to separate out even closely related varieties.

(2) *English complex:* Axis expanded, nearly straight; bracts with 7 or 8, or sometimes 9 veins, extending into the terminal third; abbreviated bract scar restricted to area immediately beneath subtended flowers; leaves with low number of dentations and lobes, though in some greater than type one. Nearly glabrous on the lower surface with hairs confined to main veins (type 1). Representative cone axis fig. 5 (ENG.).

Additional study will be necessary to determine if other varieties grown and developed in England fall into the English complex.

(3) *American complex:* Cones expanded, slightly zig-zag; bracts with 10 or more veins extending into the tip; abbreviated bract scar indistinguishable from that of type 2; leaves with high number of dentations and lobes when mature, hairs on the lower surface on veins of all sizes, and between veins. A representative cone axis is shown in fig. 5 (AM).

Though considerable care must be exercised in making comparisons, it is interesting to note the general correspondence between these morphological complexes and the classification of hop varieties according to the cohumulone content of the alpha-acid fraction presented by Rigby (1956). In that classification Group I

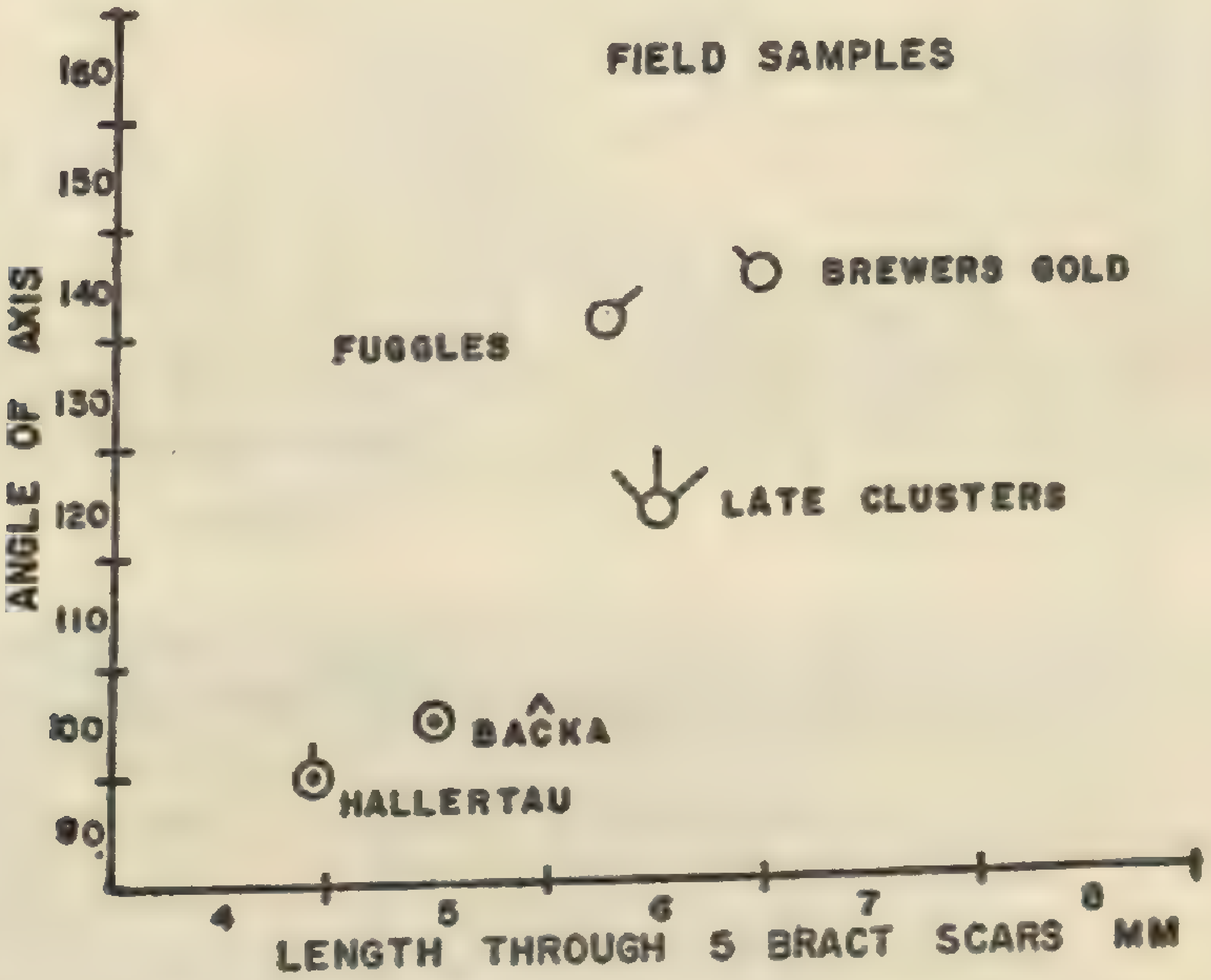

Fig. 12. Pictorialized scatter diagram of varieties indicated based upon field samples. (For explanations of symbols see p. 284).

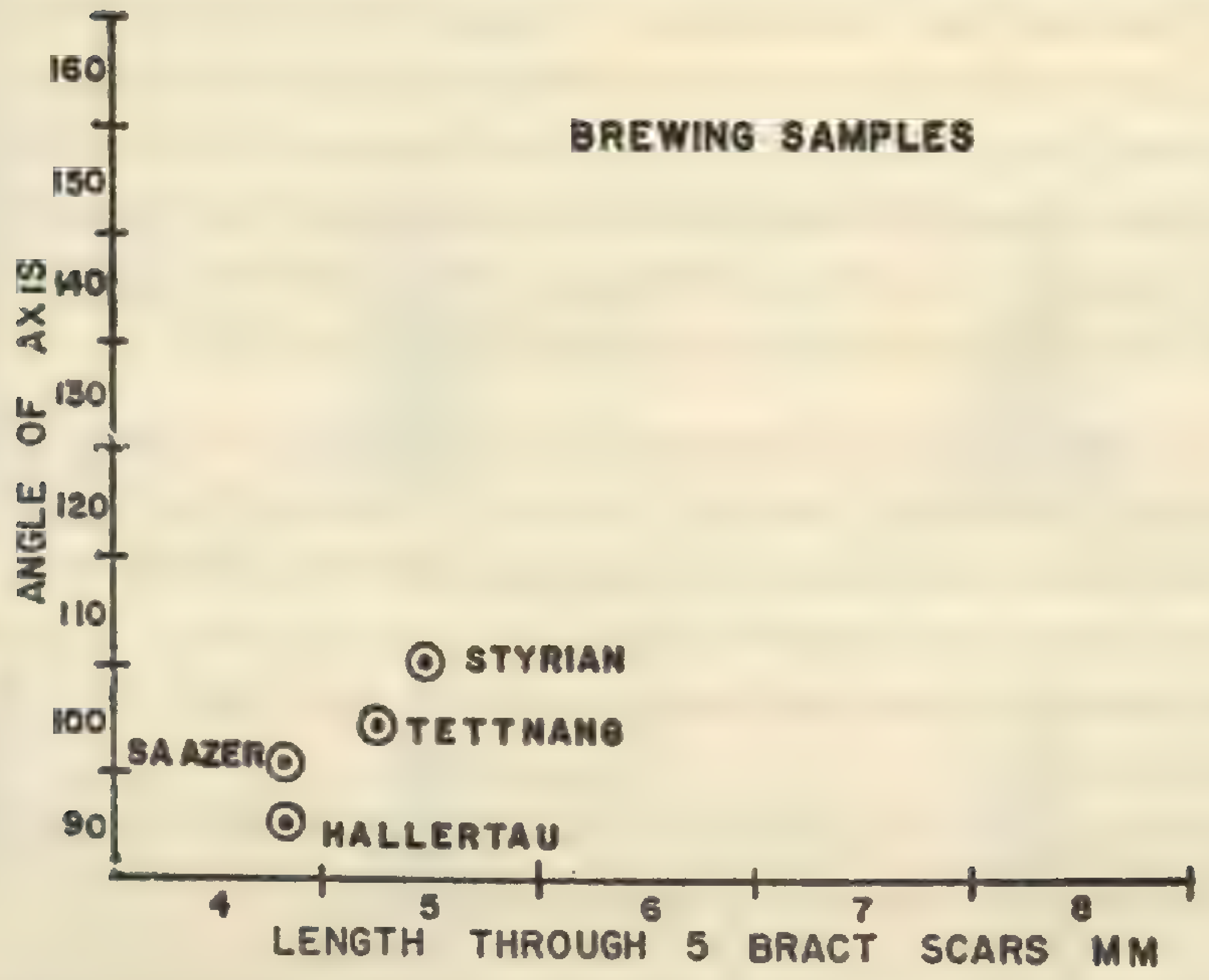

Fig. 13. Pictorialized scatter diagram of varieties indicated based upon brewing samples.

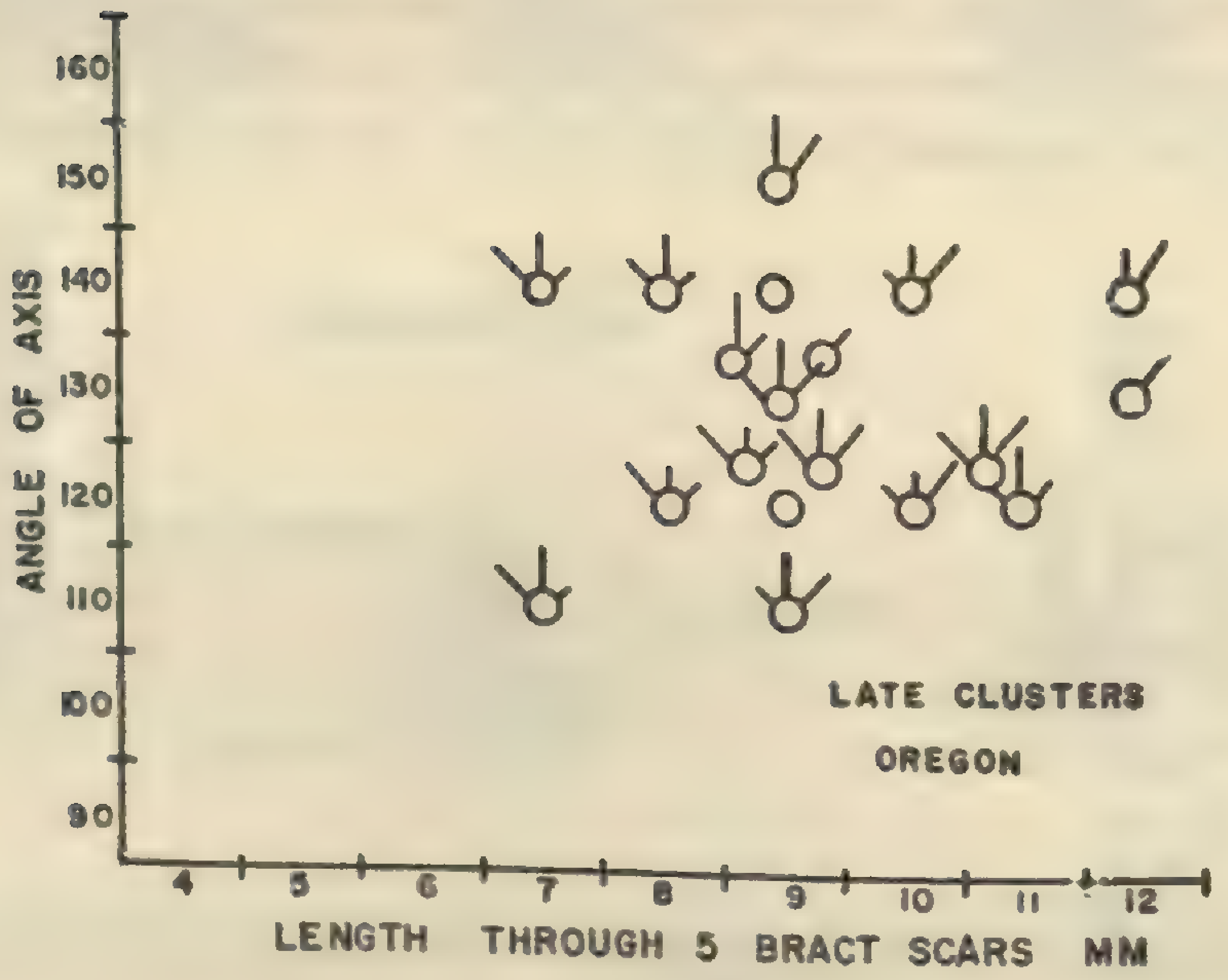

Fig. 14. Pictorialized scatter diagram of LATE CLUSTERS from poorly kept field in Oregon.

consisted of SAAZ, Bavarian and British Columbia HALLERTAU, Yugoslavian and Washington BACKA, and TETTNANG. This corresponds to complex 1, with the exception of the variety STYRIAN, which was placed as the extreme in that complex. In the classification based upon the cohumulone content, STYRIAN falls into Group II with Oregon FUGGLES and other varieties not considered here. Rigby's Group III contains among others, BREWER'S GOLD and Washington SEEDLESS (a trade name usually designating LATE CLUSTERS). Group IV consists of California and Yakima SEEDLESS (LATE CLUSTERS?). Until the same samples are examined for chemical and morphological features it will not be possible to determine the degree of agreement between the two systems, particularly for the American hops where different trade names may be used for the same variety, and a single commercial sample may contain several botanical varieties.

The American Wild Hop

Wormald's (1915) careful study of Oregon male hops led him to believe that the Oregon hop was very different from the hops of England. Consequently, Salmon and Wormald (1921) suggested the retention of the separate species *H. americanus* Nutt. Their conclusions did not receive general acceptance for these reasons: (1) The number of plants involved in the study was small. (2) It was not possible for them to make extensive analysis of either the cultivated or wild-growing American hops. (3) The various differences which they found were not sharp enough to separate the English and American hop, and the comparison was not carried to hops cultivated in other countries.

It now appears, however, that there are differences between the American culti-

Fig. 15. Distribution of wild hop types in the United States. Scored in the same manner as the cultivated hops, but based upon herbarium specimens of wild-growing hops.

vated varieties LATE CLUSTERS and other varieties cultivated throughout the world which can also be found between American wild hops and the wild hops of Europe.

In the present study, characters generally different from those used by Wormald (1915) suggest a unique American cultivated hop. In the analysis of presumably wild hops represented by herbarium material it has not always been possible to make the same sort of measurements of these characters as used in the study of field collections of cultivated plants. All too often, herbarium material is incomplete and does not permit examination of both cones and foliage. For those specimens where complete measurements were possible, the results for the United States are shown in fig. 15, using the same symbols as in the pictorialized scatter diagrams. Fig. 16 shows the distribution of pubescence types in the United States.

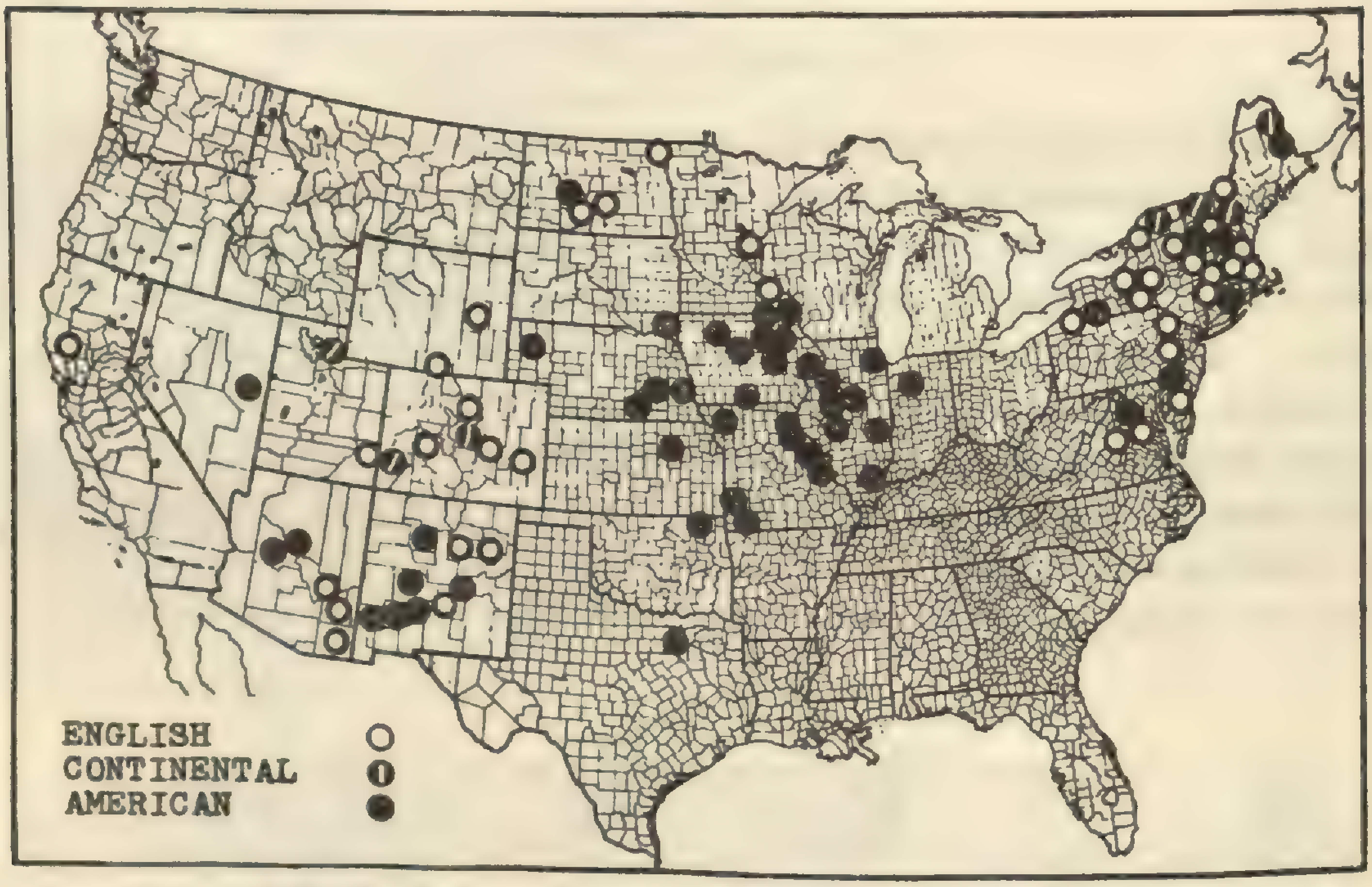

Fig. 16. Distribution of the three pubescent types of hops in the United States.

I have observed the pubescence type three, so predominant in the United States elsewhere only in specimens from Japan, possibly as a result of introduction from the United States. It is known that American hops have been imported into that country (Ehara, 1955).

Considered together, these maps bring out several interesting points. The midwestern hop is the most uniform in the country, and resembles the cultivated variety LATE CLUSTERS. Forms from both the East and the Southwest are more variable. In the East, this condition is at least partly due to escapes from cultivation, since the region was once an important area of cultivation. Such escapes are certainly much less frequent in the Southwest. Very possibly many of the types found in that area are truly indigenous, in which case LATE CLUSTERS represents only a portion of the variability of the American wild hop.

To the morphological differences between the American and European hop can be added cytological differences. Ono (1955) found the Sinoto type sex chromosome complex in Japanese and American wild hops, but not in European wild ones. An examination of a few specimens from plants for which he had determined the chromosome type showed a correlation of the American morphological type and the Sinoto type sex chromosomes. More extensive cytological investigation is required to confirm this but it lends support to the separateness of the American hop. However, the differences between the American and European wild hop, though distinct, are so slight that it would not seem advisable to establish separate names. Furthermore, until the limits of variability within the American segregate are more clearly understood, as well as the relation of the American and the Japanese plant, it is preferable to use the name *Humulus lupulus* for all wild perennial hops.

Summary

1. The nomenclatural problem in the genus *Humulus* has been reviewed. Particular attention has been devoted to efforts to establish an American taxon. It has been shown that the various characters previously did not conclusively establish a native American hop distinct from the hop of Europe.

2. Due to the ease with which the perennial hop escapes from cultivation, it is suggested that the wild and cultivated plant must be studied simultaneously.

3. A method for measuring hop variation, based upon leaves and cones, is described and applied to collections of cultivated plants, brewing samples, and herbarium material. The measured characters are shown to be stable for each variety over a wide geographical range. The cultivated hops are found to fall into three morphological complexes. One is represented by English varieties, another by German-Czechoslovakian varieties, and the third by the American variety LATE CLUSTERS.

4. An examination of the presumably wild hops in the United States shows that there are characters in common between them (and the wild hops of Japan) and the cultivated variety LATE CLUSTERS, which are unknown in European hops. This is in apparent agreement with Ono's finding of the Sinoto type sex chromosome complex in American and Japanese wild hops, but not among European ones. However, though the wild hop is uniform in the midwestern area of Illinois, Missouri, and Iowa, it is very variable in the Southwest, where it is known to be indigenous. It is at present not possible to set the limits on the variation in the truly native American hop so as to exclude all European ones. Moreover, the differences between hops from Europe and the United States are such that both vegetative and fruiting material (so often absent on herbarium specimens) are essential for a proper identification. Consequently, it is recommended that the name *Humulus lupulus* L. be applied to all perennial hops, at least until such time as the native American hop is more thoroughly understood.

Acknowledgment.—Appreciation is expressed to the Brewing Industries Research Institute and the Fixed Committee on Hop Studies for their assistance and financial support in this investigation, and to the curators of the herbaria of the Bailey Hortorium, of Harvard University, and of the Missouri Botanical Garden, who have lent specimens for this study.

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ANDROCALYMMA, A NEW GENUS OF THE TRIBE CASSIEAE (CAESALPINIACEAE)

JOHN D. DWYER*

Androcalymma Dwyer, gen. nov.

Arbores. Folia imparipinnata foliolis petiolulatis alternis vel oppositis tenuiter coriaceis costa supra immersa. Flores cymulis in paniculam terminalem dispositi. Sepala 5 imbricata; petala 5 imbricata unguiculata intus carinata. Stamina 4 libera aequalia partim circum pistillum disposita antheris biporosis rectis vel deflexis subversatilibus connectivo gracillimo. Ovarium subsessile complanatum ovulis paucis.

Trees. Leaves imparipinnate, the leaflets alternate or opposite. Flowers in cymules in a terminal panicle. Stamens 4, equal, the anthers erect or deflexed, subversatile, the connective slender. Pistil subsessile with few ovules.

Type Species: *Androcalymma glabrifolium* Dwyer.

Androcalymma glabrifolium Dwyer, sp. nov.

Arbores circ. 30 m. altae. Ramuli ultime valde lenticellati teretes glabri. Petioli 3–6 cm. longi, 0.1–0.5 cm. lati, plani glabri; stipulae non visae. Folia aequilateralia ovato-elliptica, 4.5–10 cm. longa, 2.5–5.5 cm. lata, plus minusve apice acuta basi obtusa tenuiter coriacea supra nitidula laevia glabra costa infra immersa prominente basi circ. 1.5 mm. lata, venis principalibus secundariis 8–12 prominulis arcuatis venulis laxis reticulatis marginibus parum callosis; petioluli 5–7 mm. longi graciles glabri. Flores in cymulis paucifloris dispositi, rhachidibus evidenter quam superioribus foliis brevioribus gracilibus basi ad 1.5 mm. latis basi articulatis; bracteae bracteolae caducae cicatricibus prominentibus. Sepala 5 aestivatione valde imbricata inaequalia oblonga vel ovato-oblonga circ. 3 mm. longa 1.8–2 mm. lata apice obtusa extus pubescentia ciliis mediis saepe densius dispositis intus glabra carnosa marginibus sparse ciliolatis; petala 5 subaequalia aestivatione valde imbricata oblonga 4–6.5 mm. longa 1.7–2 mm. lata apice obtusa basi unguiculata, unguibus ad 0.5 mm. longis, extus pubescentia intus glabra et evidenter carinata; stamina 4 filamentis subcrassis saepe subclavatis rectis, 2–3 mm. longis circ. 0.25 mm. in medio latis glabris mox deciduis; antherae ovato-subrotundae circ. 0.6 mm. longae vix apice biporosae subrectae vel deflexae subversatiles, connectivo circ. 0.2 mm. longo paullum thecis obscurato, 4-locellatae at 2 loculis; ovarium vix stipitatum vel subsessile complanatum oblongum circ. 2 mm. longum leviter omnino pubescens 2–3-ovulatum stylo brevissimo. Fructus non visi.

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*St. Louis University and Missouri Botanical Garden, St. Louis, Mo.

Issued January 29, 1958.

Type Collection: *Krukoff 9005*, Municipality São Paulo de Olivença; basin of Creek Belém, terra firma, high land, Amazonas, Brazil (HOLOTYPE MO, isotype NY).

The fancied resemblance of the anthers when deflexed to a drawn cowl suggested the name, *Androcalymma*.[1] The pinnately compound leaves and the porocidally dehiscent anthers readily place it in the tribe Cassieae. Several floral characters point to its relationship with *Dicorynia* Benth. and *Martiusia* Benth. of the same tribe: the imbricate sepals and petals borne on a fleshy receptacle, the lack of an obvious hypanthium, the few stamens only partially surrounding the ovary, and the very shortly stipitate ovary. The flowers disposed in numerous few-flowered cymules and the imparipinnate leaves with alternate or opposite leaflets likewise suggest this relationship. Both *Martiusia* and *Dicorynia* are well distributed in the Amazon Basin as well as in the Guianas.

Several features of the androecium as well as the very short style of the pistil serve to distinguish *Androcalymma* from its allies. The filaments of the new genus are much more elongate than those of *Martiusia* and obviously less crassate than those of *Dicorynia*. The latter genus has only two stamens. The anthers of *Martiusia* are subulate and acuminate. *Dicorynia*, with unequal filaments, has larger anthers which are 4- or 8-locellate. The presence of 8 locelli in one or in both of the anthers distinguishes *Dicorynia* from all other genera of the Caesalpiniaceae.

Worthy of special note is the slender attenuate filament tip attached to the anther of *Androcalymma*. This usually lies well hidden between the locules which are free at the base. It is difficult to trace the filament tip to the point of insertion on the connective, the base of the latter being well above the base of the locules. The subversatile condition of the anthers is apparently found elsewhere in the tribe Cassieae only in occasional species of *Cassia*.

Krukoff, the collector of the type material, notes that the tree is 100 feet high, and that the trunk measures 18 inches in diameter.

I wish to acknowledge the help of several specialists who made notations on the herbarium sheets and carried on correspondence concerning the new genus. These include: A. Ducke, R. Schery, J. Monachino, N. Y. Sandwith, and R. Cowan. Special thanks are due the last three.

[1] ’ανήρ (man); κάλυμμα (cowl).

Fig. 1. *Androcalymma glabrifolium* Dwyer

A REVISION OF THE GENUS *STYLOSANTHES**

ROBERT H. MOHLENBROCK**

History of the Genus

The genus *Stylosanthes* was established in 1788 by O. Swartz[1] with two species, *S. procumbens* (= *S. hamata* (L.) Taub.) and *S. viscosa*. Previous to the founding of the genus, most present-day species of *Stylosanthes* had been referred to other genera. Linnaeus[2] in 1753 had described *Trifolium biflorum* (= *S. biflora* (L.) BSP.) and in 1759[3] *Hedysarum hamatum* β (= *S. viscosa* Sw.); in 1775 Aublet[4] had named *Trifolium guinanense* (= *S. guyanensis* (Aubl.) Sw.).

Preceding the advent of the binomial system, a few polynomials had been applied to modern species of *Stylosanthes*. Apparently the first mention of a species now known to belong to the genus was in 1696 when Sir Hans Sloane[5] listed *Anonis non spinosa, minor, glabra, procumbens, flore lutea* as occurring in Jamaica. This is *S. hamata* (L.) Taub. In 1737 Burmann[6] recorded *Trifolium procumbens zeylanicum hirsutum* (= *S. fruticosa* (Retz.) Mohlenbrock).

Willdenow, in the fourth edition of 'Species Plantarum',[7] listed five species of *Stylosanthes*. G. Don[8] in 1832 listed thirteen species. Of these, however, only seven have proved to be distinct, and three of these were recorded without usage of the earliest epithet applicable.

The first study of *Stylosanthes* was a synopsis by Vogel[9] in 1838. He divided the genus into two sections, EUSTYLOSANTHES and STYPOSANTHES, based on the absence or presence, respectively, of an axis rudiment (an aborted secondary axis associated with each flower). An unfortunate situation has arisen, however, since Vogel designated *S. procumbens* Sw. (= *S. hamata* (L.) Taub.) of § STYPOSANTHES to be the type species. According to present nomenclatorial rules, the section or subgenus including the type species must repeat the generic name, hence Vogel's § STYPOSANTHES must be changed to § STYLOSANTHES; his § EUSTYLOSANTHES here is renamed § ASTYPOSANTHES. In his section including species without axis rudiments, Vogel recorded eight species, three of them new, while in the other section, seven species are listed including four new ones. All seven of Vogel's new

[1] Swartz, O. Prod. Veg. Ind. Occ. 108. 1788.
[2] Linnaeus, C. Sp. Pl. 773. 1753.
[3] Linnaeus, C. Syst. Nat. 10:1170. 1759.
[4] Aublet, F. Pl. Guian. 776. 1775.
[5] Sloane, H. Cat. Pl. 1696.
[6] Burmann, J. Thes. Zeyl. 1737.
[7] Willdenow, C. Sp. Pl. 3:1166. 1800.
[8] Don, G. Gen. Syst. 2:281. 1832.
[9] Vogel, in Linnaea 12: 68. 1838.

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species are recognized in this study as valid, with only one of the entire fifteen listed by him placed in synonymy.

Between 1838 and 1890, six species were ascribed to *Stylosanthes* by various authors, but all apply to species previously named.

A more detailed revision was provided by Taubert[10] in 1890, including morphology, generic relationships, and geographical distribution in addition to keys and descriptions for the species. He retained Vogel's division of the genus into two sections and recognized 22 species, four of which he himself proposed. Fifteen of these are maintained in this study, although the specific concept has changed somewhat. It is apparent that Taubert was handicapped by the limited number of specimens available for his study.

Little was added to the genus until 1919 when Hassler[11] enumerated the species of Paraguay and added fourteen subspecies, varieties, and forms to *S. guyanensis* and *S. montevidensis*.

Blake described thirteen species between 1920 and 1926, Harms[12] added one in 1923, Macbride[13] one in 1943, and Standley and Williams[14] one in 1950. In 1943, Herter[15] split the genus into two genera, *Stylosanthes* and *Astyposanthes*, equivalent to Vogel's sections and in which rank I prefer to treat them. In the present study, 25 species are recognized, three described for the first time.

Generic Relationships

Stylosanthes belongs to the tribe Hedysareae of the papilionaceous Leguminosae characterized by monadelphous stamens and a lomentum. The alternation of sub-basifixed and versatile anthers and the absence of stipels suggest its relationship with three other genera, *Zornia*, *Arachis*, and *Chapmannia*. The quartet is grouped in the subtribe Stylosanthinae.

Stylosanthes shows a close affinity with *Zornia* because of the large bracts subtending each flower and the often spicate inflorescence. The leaflets of *Zornia*, however, are paripinnate, the ovules are numerous, and bracteoles are lacking. *Arachis* is closely allied to *Stylosanthes* since both genera have similar stipules and 2–3 ovules per carpel, but they differ in that bracteoles are lacking and the loment matures underground in *Arachis*. The monotypic *Chapmannia* from Florida bears imparipinnate leaves, but differs in that it possesses minute stipules, numerous ovules per carpel, and lacks bracteoles.

Morphology

Species of *Stylosanthes* usually are herbaceous or suffruticose perennials, some attaining a height of 1.5 meters. Some species are prostrate and spreading (*S. viscosa*, some specimens of *S. hamata*), others upright and ascending. The roots usually are thick and mostly straight, with few secondary roots.

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[10] Taub. in Verh. Bot. Brand. 32:1–32. 1890.
[11] Hassl. in Fedde, Rep. Sp. Nov. 16:221–223. 1919.
[12] Harms, in Fedde, loc. cit. 19:69. 1923.
[13] Macbr. in Field Mus. Publ. Bot. 13^3:411. 1943.
[14] Standl. & L. Wms. in Ceiba 1:145. 1950.
[15] Hert. in Rev. Sudamer. Bot. 7:209. 1943.

Fig. 1. Loments of *Stylosanthes*

1. *Stylosanthes capitata, Williams & Assis 5834*; 2. *S. bracteata, Jörgensen 4877*; 3. *S. calcicola, Small 6537* (TYPE); 4. *S. mexicana, Schaffner 579* (TYPE); 5. *S. erecta, Robertson 32*; 6. *S. scabra, Martius 1124*; 7. *S. scabra, Pickel 2556*; 8. *S. tuberculata, Shafer 2463*; 9. *S. sympodialis, Weberbauer 5936*; 10. *S. fruticosa, Mearns 1956*; 11. *S. subsericea, Standley 12110*; 12. *S. macrocarpa, Pringle 6721* (TYPE). All figures × 3½.

The stems are generally diffusely branched and woody at the base, rarely simple (*S. bracteata*). The indument of the stems is diverse.

The leaves of *Stylosanthes* are trifoliolate with the terminal leaflet slightly larger than the lateral ones. They are borne at the base of the cleft of the bidentate stipules. There are no stipels. The petioles range from 1.5 to 9 mm. long. The leaflets vary considerably interspecifically in shape and size. They are borne on rhachises which seldom exceed 2 mm. in length. *S. capitata* and *S. guyanensis* may have leaflets up to 4 cm. long and nearly 2 cm. broad. In most species the leaflets are elliptic to lanceolate, obtuse to acute, occasionally mucronate, and tapering to the base. Some species have black-punctate leaflets.

The upper surface of most leaflets is glabrous, although in some species it may be appressed white-hairy. The lower surface may be glabrous, puberulent, or bristly, at least along the costa. The nerves of the leaflets usually are prominent on both surfaces.

The stipules are amplexicaul, pubescent, and bidentate at the apex. They are 3- to 11-nerved, with usually one to three nerves extending into each tooth. The stipular teeth usually are shorter than the sheath. In this study, the teeth are measured from their tip to the base of the cleft while the sheath is measured from the cleft to the base of the sheath.

The inflorescence is a terminal or occasionally an axillary spike or head. In some species the inflorescence may be elongate to 20 cm. and interrupted. The number of flowers varies from one to forty or more. The flowers are sessile in the axil of the bract and adnate to it.

Each flower is surrounded by a series of bracts and bracteoles. The outermost bract is similar to the stipules in being comprised of a 3- to many-nerved sheath with a bidentate apex from which arise one or three reduced leaflets which are identical to the cauline leaflets except in size. In some species (*S. bracteata*, *S. capitata*, *S. angustifolia*), the leaflet is reduced and the sheath is often much larger than the stipular sheaths. Within the bract is a somewhat smaller outer bracteole which usually is 3-nerved and ciliate along its margin. Inside this may be found a densely ciliate axis rudiment (§ STYLOSANTHES) or this may be lacking (§ ASTYPOSANTHES).

The nature of the axis rudiment has been the subject of much conjecture, but studies show it probably to be the vestige of a secondary floral axis. In some specimens of *S. bracteata*, the axis rudiment is adnate to the outer bracteole for about one-third of its length. Essentially the same situation occurs in *Vicia monanthos*, according to Svenson.[16] Within the axis rudiment are one (§ ASTYPOSANTHES) or two (§ STYLOSANTHES) inner bracteoles which often are deeply cleft and usually long-ciliate near the apex.

The calyx is comprised of an elongated tube expanded into five lobes at the apex. The lobes usually are unequal, with one larger than the others or rarely with two larger. Usually the four smaller lobes are connate. The largest lobe usually

[16] Sven. Am. Jour. Bot. 33:394–498. 1946.

Fig. 2. Loments of *Stylosanthes*

1. *S. nervosa*, *Weberbauer 6215* (TYPE); 2. *S. hamata*, *Ricksecker 47*; 3. *S. hamata*, *Blake 7792*; 4. *S. hamata*, *Leonard 8797*; 5. *S. sericeiceps*, *Jahn 678* (TYPE); 6. *S. biflora*, *Fisher s. n.*; 7. *S. guyanensis*, *Martius 1123*; 8. *S. angustifolia*, *Burchell 9004*; 9. *S. leiocarpa*, *Herter 89069*; 10. *S. cayennensis*, *Broadway 972* (TYPE); 11. *S. viscosa*, *Miers 2963*; 12. *S. macrosoma*, *Hassler 7606*; 13. *S. humilis*, *Orcutt 4447*; 14. *S. figueroae*, *Figueroa 897* (TYPE); 15. *S. humilis*, *Palmer 25*; 16. *S. hippocampoides*, *Herter 85562*; 17. *S. montevidensis*, *Venturi 9957*. All figures × 3½.

is acute, the others obtuse or subacute. They may be puberulent or glabrous. The tube generally is glabrous. The entire calyx may be 4–15 mm. long, the tube being 3–12 mm. long.

The corolla is typically papilionaceous. The petals are usually yellow or yellow-orange and purple-striate. They are inserted near the apex of the calyx tube. The standard sometimes attains a length of 10 mm. and a width of 8 mm. It is invariably suborbiculate. The wings are somewhat shorter and narrower than the standard, usually clawed and auriculate, sometimes spurred within at the base. The keel petals are incurved and subrostrate and are slightly smaller than the wings.

The stamens are monadelphous and united into a tube which becomes split, at least partially, with age. There are ten stamens, five with small versatile anthers alternating with five bearing larger sub-basifixed anthers. The staminal tube arches into and is enclosed by the keel petals.

The single carpel has a minute terminal stigma, an elongate, usually curved style which is persistent in fruit, and a subsessile ovary which contains two or rarely three campylotropous ovules borne on marginal placentae. Only one or two of the ovules develop.

The fruit of *Stylosanthes* is a bi-articulate loment terminated by the persistent style. The upper articulation is almost always fertile, the lower abortive or fertile. The lower articulation usually is densely pilose or glabrescent (*S. mexicana, S. leiocarpa, S. cayennensis, S. erecta*). The upper is glabrous or puberulent to sericeous or minutely tuberculate (*S. guyanensis*). The fruit usually is prominently nerved. The persistent style crowns the upper articulation as a beak which is minute or up to 8 mm. long, straight, uncinate, or circinate. The beak is glabrous or puberulent to densely villous. The relative lengths of the upper articulation and the beak are diagnostic. The upper articulation is measured from its base to a ventral protuberance formed where the upper articulation narrows into the beak. The beak, whether erect, declined, or coiled, is measured from the ventral protuberance to its maximum height as a simple vertical projection of the upper articulation. This measurement, therefore, usually does not represent the gross length of the beak but merely the distance that it projects above the upper articulation. The seeds are black, compressed, ovoid, estrophiolate.

In the latter part of the nineteenth century, a statement crept into the literature attributing two kinds of flowers to *Stylosanthes biflora*: apetalous ones from which the seeds are set exclusively, and petalous ones which are sterile. This apparently has been copied by numerous authors through the years and still persists in some of our more recent manuals. No evidence of apetalous flowers occurring in *S. biflora* was found in this study.

Geography of the Genus

The genus *Stylosanthes* is indigenous to savannas and similar areas in the eastern United States, Central America, the Antilles, South America to northern Argentina, the Galapagos Islands, central and southern Africa, Madagascar, and southern

India and Ceylon. In addition, *S. humilis* is adventive in Malaysia and Australia.

All eleven species of § ASTYPOSANTHES occur in the Western Hemisphere. Some are wide-ranging and show considerable variability, although most are well defined. Five of the seven widely distributed species of *Stylosanthes* belong in this section. *S. biflora* is rather abundant over the eastern United States. The very widespread *S. guyanensis* with its two subspecies occurs from Central America to southern Brazil and Bolivia. *S. viscosa* occurs from Baja California through Central America and northern South America and the Caribbean basin. *S. montevidensis* and its close local relatives, *S. hippocampoides* and *S. macrosoma*, center in southern Brazil, Bolivia, and Paraguay. *S. angustifolia* occurs rather frequently in northern Brazil and the Guianas. The other three species of this section, *S. cayennensis*, *S. figueroae*, and *S. leiocarpa*, are local, the first two being restricted to extreme northern South America, the last to Uruguay, Paraguay, and southeastern Brazil.

The fourteen species of § STYLOSANTHES, on the other hand, are exceedingly difficult to distinguish and are mostly restricted. Only *S. hamata* of the Antilles and *S. fruticosa* of southern Africa, India, and Ceylon are widespread. *S. scabra* is rather abundant from Colombia to Minas Geraes, Brazil. *S. macrocarpa* and *S. subsericea* are confined to Central America and *S. calcicola* to Florida, the Antilles, and parts of Central America. From Colombia and Venezuela to Peru and Ecuador are found *S. mexicana* (also in Mexico and Bolivia), *S. nervosa*, *S. tuberculata* (also in the Antilles), *S. sericeiceps*, and *S. sympodialis* (also in the Galapagos Islands). *S. bracteata* and *S. capitata* center in Brazil. *S. erecta* occurs in east-central Africa.

USES

Certain species of *Stylosanthes* (*S. fruticosa*, in particular) are used as fodder crops. In Australia, *S. guyanensis* ssp. *guyanensis* has been planted in an effort to check soil erosion. Nodules of nitrogen-fixing bacteria are present on the roots of most of the species. Data for some specimens indicate *Stylosanthes* to be a good cover crop for coffee.

Several folk uses are attributed to certain members of the genus. Taubert noted that a few species have been used as diuretics. Hutchinson and Dalziel[17] attribute many uses for *S. erecta* by native Africans:

> In Gambia an infusion of the plant is taken internally for colds, etc. In N. Nigeria the odorous smoke produced in a pipe is blown on to arrow wounds as an antidote to their poison. The plant is a common ingredient in superstitious herbal practice, *e.g.*, the root worn as a charm or prepared as a wash is a preventive of injury by sharp weapons (Hausa *maganin k'arfe*, literally "medicine against metal"). Other plants with hard roots are similarly employed (*e.g.*, *Uraria picta*). It is an ingredient in aphrodisiac prescriptions. A decoction of the root or leaf used as a daily bath for an infant will enable him to walk very early. The plant, smoked like tobacco, and also made into a decoction, is a charm against injury by a blow by a cudgel, and will cause the weapon to break.

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[17] Appendix to Fl. W. Trop. Afr. p. 262. 1937.

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Systematic Treatment

Stylosanthes Sw. Prod. Veg. Ind. Occ. 108. 1788. (T: S. *hamata* (L.) BSP.)

Astyposanthes Hert. in Rev. Sudamer. Bot. 7:209. 1943.

Herbs, rarely subshrubs. Leaves pinnately 3-foliolate; stipules amplexicaul, divided at the apex into two teeth, adnate to the base of the petioles; stipels none. Inflorescence spicate, terminal or axillary, 1- to several-flowered; flowers yellow or orange with purple stripes; calyx 5-lobed and with a long tube; corolla 5-merous, papilionaceous; stamens 10, the filaments united into a tube which splits with age, with 5 versatile anthers alternating with 5 sub-basifixed anthers; fruit a 1- to 2-articulated loment; seeds ovoid, light brown to black, smooth, lustrous.

The herbaria in which the cited specimens are deposited and their abbreviations are as follows: Chicago Natural History Museum (F), Gray Herbarium (GH), Missouri Botanical Garden (MO), New York Botanical Garden (NY), and the United States National Herbarium (US).

KEY TO THE SPECIES

Sect. I. STYLOSANTHES. Each flower, or at least the lower flowers, subtended by an axis rudiment; inner bracteoles 2 (1 in S. *sericeiceps*).

A. Bracts 13–25 mm. broad, with 13–23 conspicuous and usually broad, colored nerves.
  B. Fertile articulations of the loment often 2, the upper glabrous, the beak less than one-third as long as the upper articulation, glabrous or with a very few short stiff hairs; nerves of the bracteal sheath about 15; stems usually with scattered bristles. Brazil, Venezuela.........1. S. *capitata*
  BB. Fertile articulations of the loment 1, pilose, the beak only slightly shorter than the upper articulation, pilose; nerves of the bracteal sheath about 21; stems pilosulous to villous. Brazil, Paraguay.........2. S. *bracteata*
AA. Bracts at most 10 mm. broad, with fewer than 15 nerves which are inconspicuous.
  C. Beak of the loment straight or only slightly curved; leaflets glabrous on both surfaces (rarely with marginal cilia); teeth of the upper stipules mostly longer than the sheath. Florida, Central America, Mexico, Bahamas, Cuba.........3. S. *calcicola*
  CC. Beak of the loment uncinate or coiled; leaflets usually pubescent, at least on the lower surface (occasionally glabrous in S. *erecta* of Africa and S. *hamata* of the West Indies); sheath of the upper stipules mostly longer than the teeth.
    D. Loment completely glabrous or with some pubescence on the beak only or occasionally on the nerves in S. *mexicana*.
      E. Stems sericeous or bristly; leaflets sparsely but conspicuously bristly-ciliate; loment often green, with both articulations usually fertile; inflorescence obovoid. Mexico, Venezuela, Bolivia.........4. S. *mexicana*
      EE. Stems glabrous or puberulent above; leaflets without bristly cilia; loment brown, with only one articulation usually fertile; inflorescence often narrow. West Africa.........5. S. *erecta*
    DD. Loment pubescent on the body and usually on the beak.
      F. Stem and bracts bearing tuberculate-based hairs (sometimes merely with tubercles); lower surface of leaflets usually villous with interspersed tuberculate bristles; beak

of the loment shorter than the upper articulation (sometimes equaling it in S. *macrocarpa* and S. *nervosa*).

G. Beak of the loment half to one-third the length of the upper articulation.

H. Bracts shortly scabrous-hispid; inflorescence usually nearly as broad as long; beak of the loment short-hairy.

I. Leaflets often punctate beneath, obtuse; stem bearing short dark setae, the whole aspect of the plant dingy brown; fertile articulation usually 1, pubescent throughout. Brazil, Ecuador, Venezuela, Colombia, Bolivia. ....6. S. *scabra*

II. Leaflets not punctate beneath, acute; stem setose or puberulent to densely pilose, not dingy brown; fertile articulations often 2, pilosulous only on the ribs. Bahamas, Cuba, Colombia, Venezuela, Peru........7. S. *tuberculata*

HH. Bracts villous or with long tuberculate bristles; inflorescence often 2–3 times longer than broad; beak of the loment usually rufous-pilose.

J. Bracts softly villous and rarely with tuberculate bristles; inflorescence 2–3 times longer than broad; loment 1.0–1.5 mm. broad, the beak rufous-pilose. Ecuador, Peru, Galapagos Islands........8. S. *sympodialis*

JJ. Bracts with tuberculate bristles; inflorescence about as broad as long; loment 1.5–2.5 mm. broad, the beak puberulent. Africa, Ceylon, India. ....9. S. *fruticosa*

GG. Beak nearly equaling to exceeding the upper articulation.

K. Beak of the loment strongly coiled; bracteal sheath and often the stem sericeous and with interspersed tuberculate bristles. Honduras, Mexico........10. S. *subsericea*

KK. Beak of the loment curved to strongly uncinate; bracteal sheath and stem with tuberculate bristles but not sericeous.

L. Upper articulation and beak combined about 8 mm. long, the beak about equaling the upper articulation; plants to 0.2 m. tall. Mexico.....11. S. *macrocarpa*

LL. Upper articulation and beak combined 5.0–7.5 mm. long, the beak sometimes slightly shorter than the upper articulation; plants to 1 m. tall.

M. Fertile articulations mostly 2; bracteal sheath usually bearing long tuberculate-based bristles; leaflets elliptic, obtuse to subacute, usually puberulent. Africa, Ceylon, India........9. S. *fruticosa*

MM. Fertile articulation usually 1; bracteal sheath short-hispid to densely ciliate; leaflets usually oblanceolate, acute to acuminate, glabrous or occasionally hispid beneath. Venezuela, Peru, Bolivia, Argentina. ....12. S. *nervosa*

FF. Stem and bracts pilose, villous, or nearly glabrous, lacking tuberculate bristles; lower surface of leaflets pilose or appressed-villous or glabrous, never with tuberculate bristles; beak of the loment equaling or exceeding the upper articulation (except S. *sericeiceps*).

N. Beak of the loment equaling or exceeding the upper articulation; pubescence of the bracteal sheath whitish; stem usually not pubescent throughout. Florida, Bahamas, Cuba, Central America, Colombia, Venezuela........13. S. *hamata*

NN. Beak of the loment about one-half as long as the upper articulation; pubescence of the bracteal sheath tan or rufous; stem often pubescent throughout.

O. Loment pubecsent throughout; leaflets glabrous above, 15–25 mm. long; bracteal sheaths tan-pilose. Venezuela........14. S. *sericeiceps*

OO. Loment pubescent above, glabrous below; leaflets minutely pubescent above, 20–40 mm. long; bracteal sheaths rufous-pilose. Peru, Ecuador, Galapagos Islands........8. S. *sympodialis*

Sect. II. ASTYPOSANTHES. Flowers not subtended by an axis rudiment; inner bracteole 1.

A. Beak of the loment minute, at most about one-fifth as long as the upper articulation, the fertile articulation 1.

B. Fertile articulation shortly hairy throughout or rarely glabrous, terete, 2.5–5.0 mm. long. Eastern United States........15. S. *biflora*

BB. Fertile articulation minutely tuberculate near the apex or rarely with a few scattered appressed white hairs, flattened, 1.5–3.0 mm. long. Bahamas, Central America, Mexico, South America........16. S. *guyanensis*

AA. Beak of the loment from one-fourth as long to exceeding the upper articulation, the fertile articulations 1–2.

C. Leaflets 0.5–2.0 mm. broad; inflorescence very narrow and elongate; beak of the loment strongly uncinate, often 2–3 times as long as the pubescent upper articulation. Brazil, Guianas....................17. *S. angustifolia*

CC. Leaflets 2–6 mm. broad; inflorescence usually capituliform, globose to ovoid or obovoid; beak of the loment various but not strongly uncinate.

D. Loment glabrous (occasionally pubescent only on the beak).

E. Loment with 2 fertile articulations, the beak straight or uncinate; bracteal leaflets stalked.

F. Beak straight or nearly so, about equaling the upper articulation, together about 5–6 mm. long; bracts, leaflets, and stems densely short-bristly. Brazil, Uruguay, Paraguay....................18. *S. leiocarpa*

FF. Beak uncinate, one-third as long as the upper articulation, together 3.0–3.5 mm. long; bracts and sometimes the leaflets and the stems with scattered long bristles, often glabrous. French Guiana....................19. *S. cayennensis*

EE. Loment with 1 fertile articulation, the beak strongly uncinate to coiled; bracteal leaflets sessile or subsessile.

G. Loment conspicuously reticulate-nerved, about as broad as long (excluding the beak); inflorescence 4- to 8-flowered. Uruguay, Argentina....................20. *S. hippocampoides*

GG. Loment obscurely nerved, about twice as long as broad (excluding the beak); inflorescence 2- to 4-flowered. Paraguay....................21. *S. macrosoma*

DD. Loment pubescent (if nearly glabrous, the stem viscid).

H. Beak shorter than or nearly equaling the upper articulation; stem often viscid.

I. Stems with viscid hairs or short-hispid; leaflets usually punctate beneath; fertile articulations 1–2.

J. Fertile articulations usually 2, the upper decidedly widest above the middle, the beak coiled, about one-third the length of the upper articulation. Bahamas, Cuba, Central America, Mexico, South America....................22. *S. viscosa*

JJ. Fertile articulation usually 1, broadest at or below the middle, the beak nearly straight or slightly uncinate, one-half to nearly equaling the upper articulation. Colombia....................23. *S. figueroae*

II. Stems without viscid hairs; leaflets not punctate; fertile articulation 1. Brazil, Paraguay, Uruguay, Bolivia, Argentina, Colombia....................24. *S. montevidensis*

HH. Beak nearly 2–4 times longer than the upper articulation; stems not viscid. Central America, Mexico, Bahamas, Cuba, Colombia, Venezuela, Brazil....................25. *S. humilis*

Section I. Stylosanthes

Section *STYPOSANTHES* Vog. in Linnaea 12:68. 1838. (T: *S. hamata* (L.) Taub.)

Each flower, or at least the lower, subtended by an axis rudiment; inner bracteoles 2.

Styposanthes hamata (L.) Taub., as type of the genus, automatically becomes the type of § STYLOSANTHES.

1. Stylosanthes capitata Vog. in Linnaea 12:70. 1838, ex char.

Stems erect, branched, to 1 m. tall, subligneous near the base, decumbent or ascending, densely and shortly white-hairy and also with some scattered bristles, the pubescence generally more dense below each node. Leaflets oblong to elliptic, to 30 mm. long and 15 mm. broad, usually about 15 mm. long and 5 mm. broad, acute and mucronulate at the apex, densely villous on both surfaces, with 7–9 pairs of conspicuous veins; petioles 3–6 mm. long, densely villous, the rhachis 1.0–3.5 mm. long; sheath of the stipules 7–9 mm. long, densely villous, longer than the subulate teeth, several-nerved. Spikes thick, capituliform, about two-thirds as broad as high, to 35 mm. long, many-flowered, on peduncles usually 5–7

cm. long, occasionally 2–3 cm. long; bracts with a single very reduced leaflet; sheath often purplish, 8–12 mm. broad, conspicuously 11- to 17-nerved, copiously soft-pubescent; outer bracteole 1, to 3 mm. long, ciliate; axis rudiment 5–7 mm. long in fruit, very long-ciliate; inner bracteoles 2, 2.0–2.5 mm. long and much narrower than the outer, densely ciliate at the apex. Calyx tube 4–6 mm. long, the mostly acute and sparsely ciliate lobes about 2.5 mm. long. Standard obovate, 5–7 mm. long; wings obovate, 4–5 mm. long, auriculate at the base; keel petals 3–4 mm. long, falcate and auriculate. Loment to 2.5 mm. broad, reticulate-nerved; both articulations usually fertile (either sometimes abortive), the upper about 3.5 mm. long and glabrous, the lower somewhat shorter and glabrous or sparsely pubescent; beak uncinate, about 1 mm. long, glabrous or with very few short stiff hairs on the inner face.

Taubert in his diagnosis of S. *capitata* states that the legume is uni-articulate, the lower joint being abortive. However, specimens of this species may bear two fertile articulations. The original description of S. *capitata* which contains no mention of the fruit apparently is based on an incomplete specimen, for Vogel comments: "*Vidi specimen unum incompletum*".

All species of *Stylosanthes* except S. *capitata*, S. *bracteata*, and S. *angustifolia* possess 1–3 leaflets between the teeth of the bracteal sheaths. In these three, a small laminal extension of the midvein of the sheath usually is all that is present.

Specimens from Venezuela and the Piauí state of Brazil are more coarse and have the general vegetative appearance of S. *scabra*. The nature of the inflorescence and loment clearly distinguishes S. *capitata* from S. *scabra*.

Grows in fields, forests, or waste ground and is known only from Brazil and Venezuela. It grows at altitudes of about 1000 meters. Vogel does not specifically cite any specimens but merely states that S. *capitata* has been collected in Brazil by Sellow between Victoria and Bahia (fig. 3).

BRAZIL: MARANHÃO: Rio Tocantins, *Pires & Black 1994* (NY). MINAS GERAES: Belo Horizonte, *de Oliveira s. n.* (US), *Williams & Assis 5646, 5863* (GH), *5834* (GH, MO, NY); Morro das Pedras, *Williams & Assis 6475* (GH); Pampulha, *Williams 5644* (NY). PIAUÍ: Oeiras, *Gardner 2093* (GH, NY); exact locality unknown, *Lützelburg 112* (NY).

VENEZUELA: ANZOÁTEQUI: near Mapira, *Lasser 775* (US). BOLÍVAR: Ciudad Bolívar, *Bailey 1434* (GH, NY, US).

2. STYLOSANTHES BRACTEATA Vog. in Linnaea 12:70. 1838. (T: *Sellow 4734!*)

Stems herbaceous, very slender, erect, simple or occasionally branched, to 2 dm. tall, pilosulous to villous throughout. Leaflets lanceolate to elliptic, acute to obtuse and mucronulate at the apex, to 25 mm. long and 4 mm. broad, usually much narrower, pilose on both surfaces, with 5–7 pairs of veins prominent beneath; petioles 1–2 mm. long, pilosulous, the rhachis about 0.5 mm. long; sheath of the stipules 5–8 mm. long, pilosulous or villous as the stem, 17- to 21-nerved, the teeth lance-subulate, 4.5–7.0 mm. long. Spikes capitate, 8- to several-flowered, to 30 mm. long; bracts unifoliolate, pilose and ciliate, 10–15 mm. wide, the sheaths

Fig. 3

8.0–9.5 mm. long and with 15–21 prominent purplish nerves, the teeth 2.0–3.5 mm. long, the sessile leaflet to 5.5 mm. long; outer bracteole 1, 3.0–3.5 mm. long, bifid and ciliate near the apex; axis rudiment 7–9 mm. long in fruit, very densely pilose; inner bracteoles 2, 2–3 mm. long, ciliate. Calyx tube 8.0–8.5 mm. long, the lobes 2.0–2.5 mm. long and ciliate. Standard obovate, 4.5–6.0 mm. long; wings 3.5–4.5 mm. long, auriculate at the base; keel petals 3–5 mm. long, auriculate. Loment to 2 mm. wide, reticulate-nerved; lower articulation abortive, upper articulation 3–4 mm. long, densely pilose; beak strongly uncinate, 3.0–3.5 mm. long, pilose.

The presence of the copiously and softly hairy broad bracts makes *S. bracteata* readily distinguishable from other species of the genus. This species is the most slender *Stylosanthes* and, when in fruit, possesses the longest axis rudiment. In some specimens, the axis rudiment is adnate to the outer bracteole for about one-third of its length.

In dry regions in Paraguay and southwestern Brazil at altitudes around 800 meters; may also occur in northeastern Argentina. Burkart[18] comments that specimens referable to S. *bracteata* collected by Spegazzini (*2194* and *2195*) may be from Argentina, although the labels signify only "*Norte de la provincia de Corrientes*" (fig. 3).

BRAZIL: MATO GROSSO: Capão Bonito, *Archer & Gehrt 105* (US). MINAS GERAES: Ituiutabá, *Macedo 479* (US), *1241* (MO); Uberaba, *Regnell s. n.* (US). PARANÁ: between Lagos and Desiro, *Dusén 15684* (GH); Tibagu, *Reiss s. n.* (F); Villa Velha, Ponta Grossa, *Hoehne 23369* (GH, NY). WITHOUT PRECISE LOCALITY: Rio Vardo, *Riedel s. n.* (NY); *Sellow 4734* (GH, F).

PARAGUAY: Estancia Primera, *Jörgensen 4877* (US, MO); between Río Apa and Río Aquidaban-mi, *Fiebrig 5208* (GH, US); Tapiracuay River, *Hassler 4363* (GH, NY); exact locality unknown, *Hassler 8510* (NY).

3. STYLOSANTHES CALCICOLA Small, Man. Southeast. Fl. U. S. 730. 1932. (T: *Small, Mosier, & Small 6537*!)

Stems erect, to 0.5 m. tall, branched from near the base, minutely pubescent along one side, or sometimes glabrous, rarely pubescent throughout. Leaflets lanceolate to ovate, acute or acuminate at the apex, to 15 mm. long, glabrous or ciliate on margins near the base, with 3–5 pairs of conspicuous veins; petioles 2–4 mm. long, glabrous or puberulent, the rhachis 0.2–1.0 mm. long; sheath of the stipules glabrous or puberulent, with about 7 conspicuous nerves extending into the usually somewhat longer teeth. Spikes narrowly oblong or ovoid, 0.5–1.5 cm. long, crowded, 2- to several-flowered; bracts unifoliolate, the sheath equaling to twice as long as the teeth, averaging 4 mm. wide, ciliate and often bristly on the back, 5- to 7-nerved; outer bracteole 1, about 3 mm. long, ciliate at the apex; axis rudiment 6.0–7.5 mm. long in fruit, sparsely pilose; inner bracteoles 2, 2.0–2.5 mm. long, ciliate at the apex. Calyx tube 3–4 mm. long, about 1 mm. longer than the acute lobes. Standard obovate, 4.5–6.0 mm. long; wings 4–5 mm. long, auriculate; keel petals falcate, 3.5–4.5 mm. long. Loment 1.5–2.0 mm. broad, conspicuously nerved; both articulations usually fertile, the upper 2.5–3.0 mm. long, densely and shortly white-hairy or sometimes glabrate, the lower 2.0–2.5 mm. long, puberulent or sericeous; beak straight or only slightly curved, 1.5–2.5 mm. long, from half as long to equaling the upper articulation, with short white hairs or glabrous.

Stylosanthes calcicola is distinguished from all other species of the section by its straight beak and its general lack of pubescence.

Small described S. *calcicola* in 1932 from a collection made in Dade County, Florida, in 1915. All the Florida specimens were collected in pinelands in hammocks. In addition to Florida, the species is indigenous to Mexico (Yucatan), Guatemala, and Cuba. Apparently the first collection of this species was made from Yucatan by Gaumer (*908*) in 1895 or 1896. Although there are minor differences between the Florida and Yucatan specimens, the characters of the loment

[18] Darwiniana 3:327. 1939.

and the general lack of pubescence throughout the entire plant seem to indicate that these populations belong to the same species. The specimens from Florida are mostly low, much-branched plants (tall and unbranched in *Cornman 2132*) with densely pubescent loments while those from Yucatan and Cuba are considerably taller and generally possess pubescent loments. The leaflets of the Florida specimens are shorter.

Stylosanthes calcicola resembles *S. hamata* with respect to leaflet morphology, habit, and the densely pubescent loments. It is an apparent calciphile with a tolerance for rather warm, arid climates.

United States: florida: Dade Co.: pinelands near Murden Hammock, *Small, Mosier & Small 6438* (MO); pinelands near Ross-Costello Hammock, *Small, Mosier & Small 6537* (US). Monroe Co.: Big Pine Key, *Cornman 2132* (MO).

Guatemala: huehuetenango: between Nentón and Las Palmas, *Steyermark 51654* (F).

Mexico: yucatan: Chichancanab, *Gaumer 2044* (GH, US, MO, F); Izamal, *Gaumer 992* (GH, US, F); San Anselmo, *Gaumer 1955* (GH, NY, MO, F), *Gaumer 1956* (GH, US, MO, F), *Gaumer 908* (MO, US, F); Progreso, *Flores 1* (F).

Bahamas: new providence island: West Bay, *Degener 18984* (GH, NY).

Cuba: camagüey: Ganado, Cayo Sabinal, *Shafer 863* (NY, F).

4. Stylosanthes mexicana Taub. in Verh. Bot. Brand. 32:21. 1890. (T: *Schaffner 579*!)

Stylosanthes bangii Taub. ex Rusby, in Mem. Torr. Bot. Club 4:206. 1895. (T: *Bang 936*!)

Stem ascending to spreading, subligneous near the base, to 3 dm. tall, usually much branched from near the base, densely covered with appressed white hairs, often with scattered bristles at least on the lower half of the stem. Leaflets broadly lanceolate to obovate, obtuse to subacute, glabrous or nearly so above, usually sparsely bristly-ciliate, occasionally with some tuberculate-based bristles on the lower surface, with 3–4 pairs of conspicuous veins; terminal leaflet to 16 mm. long and 4 mm. broad, the lateral leaflets somewhat smaller; petioles 3–6 mm. long, shortly white-hairy to nearly glabrous, the rhachis to 2 mm. long; sheath of the stipules equaling or exceeding the teeth, somewhat veiny, pubescent like the stem. Spikes dense, more or less oblongoid, to 15 mm. long, several-flowered; outer bracts trifoliolate, the inner unifoliolate, the sheath with short white hairs or sometimes with tuberculate-based bristles, 7- to 9-nerved, 3.5–5.0 mm. long, the teeth 0.5–1.0 mm. shorter than the sheath; outer bracteole 1, oblong-lanceolate, ciliate, bifid, 3.5–4.5 mm. long; axis rudiment to 6 mm. long in fruit, long white-ciliate; inner bracteoles 2, ciliate, 2–3 mm. long. Calyx tube to 6 mm. long, the obtuse lobes about 2–3 mm. long, usually glabrous, sometimes ciliate. Standard suborbiculate, 4.5–6.0 mm. long; wings nearly equaling the standard in length, subauriculate at the base; keel petals falcate, 3.0–4.5 mm. long. Loment 6–7 mm. long, 1.5–3.5 mm. broad, reticulate- nerved; both articulations usually fertile, the upper 3–5 mm. long, glabrous or with some appressed pilosity on the nerves when immature, the

lower somewhat shorter, glabrescent, occasionally abortive; beak recurved-uncinate or sometimes with a half-coil, 2.5–3.0 mm. long, usually about equaling the upper articulation in length, glabrous or sparsely hairy.

Stylosanthes mexicana shows much variation in leaflet shape and pubescence. While most specimens possess some tuberculate hairs in addition to simple pili, *Leavenworth 135* from Nuevo León, and *Purpus 4925* from San Luis Potosí, Mexico, lack these bristles. The leaflets of *Purpus 4925* are obtuse instead of acute.

On valley floors dissected by arroyos and alluvial fans, in wooded gorges, and savannas at altitudes from 800 to 2500 meters (fig. 3).

At first glance, the geographic distribution of S. *mexicana* seems to be very peculiar. This species is known from a few states in central Mexico and from Caracas, Venezuela, and the chacos of Bolivia, widely disjunct areas. This situation, however, occurs in several species of flowering plants, striking examples being *Larrea divaricata* (Zygophyllaceae), *Atamisquea emarginata* (Capparidaceae), and *Koeberlinia spinosa* (Koeberliniaceae). This last species is known from the Mexican states of Tamaulípas, Nuevo León, and San Luis Potosí and again from a small area in the western chacos of Bolivia.

In searching for an explanation of this seemingly unusual distribution, Johnston[19] observes that both the areas in Mexico and Bolivia are extensive regions which are characterized by low atmospheric humidity and rainfall usually less than twenty inches annually, and in which the climatic and edaphic conditions are rather similar. The plants which occur in these areas belong principally to genera of a xerophitic nature. Johnston points to the presence in the deserts of North America of floristic elements which apparently are a part of a flora now well represented in South America. He believes we are dealing "with a very old American desert flora formerly shared by both continents. In South America it is now relatively well preserved but in North America it lingers in a few recognizable remnants."

It is obvious that at the present time the extensive unbroken belt of wet tropical forest between the Mexican and Bolivian stations presents "effective barriers to the exchange of elements." Johnston postulates that "during dry, warm epochs, an exchange might have been effected along relatively arid coastal strips similar to . . . those now present in western Central America, Ecuador, and Peru."

The species from Bolivia, known as S. *bangii,* is indistinguishable from S. *mexicana* and is considered synonymous.

MEXICO: COAHUILA: Palm Canyon, *Marsh 969* (F). HIDALGO: near El Salto, *Pringle 11969* (GH, US, F). NUEVO LEÓN: Diente Canyon, near Monterrey, *Mueller & Mueller 325* (F); Monterrey, *Pringle 2253* (GH, F); Villa de Santiago, *Leavenworth 135* (MO). OAXACA: Mitla, *Smith 101* (US). QUERÉTARO: San Juan del Río, *Rose, Painter & Rose 9528* (US). SAN LUIS POTOSÍ: Mina de San Rafael, *Purpus 4928* (GH, NY, MO, F); San Miguelito, *Schaffner 800* (GH, NY), *579* (US, F). TAMAULÍPAS: Buena Vista Hacienda, *Wooton s. n.* (US); Cerro de la Tamaulípeca, *Bartlett 10608* (F), *10612* (GH, F); near Miquihuana, *Stanford, Retherford & Northcraft 793* (GH, NY, MO); vicinity of La Victoria, *Palmer 490* (GH, NY, US); exact locality unknown, *Viereck 300* (US).

BOLIVA: COCHABAMBA: Bolivian Plateau, *Bang 963* (GH, NY, MO, US, F).

[19] Jour. Arn. Arb. 21:356–363. 1940.

VENEZUELA: DISTRITO FEDERAL: Caracas, *Pittier 9679* (GH, US, NY); lower Catiza, near Caracas, *Pittier 7319* (GH, US).

5. STYLOSANTHES ERECTA Beauv. Fl. Owar. 2:28. 1807, ex char.

Stylosanthes guineensis Schum. in Schum. & Thonn. Beskr. Guin. Pl. 357. 1828, ex char.
Ononis coriifolia Reichb. ex Guil., Perr. & Rich. Pl. Senegam. 204. 1830, nom. nud. in synon.
Stylosanthes guineensis G. Don, Gen. Syst. 2:281. 1832, ex char.
Stylosanthes erecta var. *guineensis* Vog. in Linnaea 12:68. 1838, ex char.
Stylosanthes erecta var. *acuminata* Welw. ex Baker, in Oliver, Fl. Trop. Afr. 2:156. 1871, ex char. (T: *Welwitsch 2127*.)

Stems suffrutescent, suberect, 0.3–1.5 m. tall, much branched, puberulent above, glabrous below, rarely with bristles. Leaflets oblanceolate, mucronulate, narrowed at both ends, glabrous, often punctate beneath, usually with 2–5 pairs of conspicuous veins; terminal leaflet to 25 mm. long and 5.5 mm. broad, the lateral ones to 13 mm. long and 4.5 mm. broad; petioles 4–6 mm. long, glabrous or puberulent, the rhachis about 1.5 mm. long; sheath of the stipules 4.0–7.5 mm. long, glabrous, puberulent, ciliate, or bristly, 5- to many-nerved, the teeth 3.5–5.0 mm. long. Spikes oblongoid to narrowly elongate and sometimes interrupted, 4- to 12-flowered; bracts usually unifoliolate, the leaflet averaging 6 mm. long, the sheath 4–6 mm. long, 4.0–5.5 mm. broad, ciliate along the margins and often bristly on the back, 5- to 7-nerved, the teeth 2.5–4.5 mm. long; outer bracteole 1, 3–6 mm. long, ciliate at the apex; axis rudiment 3.5–6.5 mm. long, ciliate; inner bracteoles 2, 2.0–3.5 mm. long. Calyx tube 4.0–5.5 mm. long, the lobes about 2 mm. long. Standard suborbiculate, 4.0–6.5 mm. long; wings 4–5 mm. long, auriculate, clawed; keel petals falcate, 3.5–4.5 mm. long. Loment 1.5–2.0 mm. wide, reticulate and with one longitudinal nerve per face; only the upper articulation usually fertile, 3.5–4.5 mm. long, glabrous or nearly so; beak uncinate, glabrous or short-hairy on the inner face, 1.5–2.5 mm. long, less than half as long as the upper articulation.

Stylosanthes erecta is distinguished by its loments which are mostly uni-articulate and glabrous or nearly so, although the illustration which accompanies Beauvais' original description depicts a bi-articulate loment.

The shape and pubescence of the leaflets are quite variable and have given rise to two named varieties regarding which there has been considerable confusion. Taubert cites *Welwitsch 2127* under var. *guineensis*, but this specimen is the type for var. *acuminata*. Var. *guineensis* is usually applied to those specimens which have bristly stems. Although including var. *guineensis* in his 'Leguminosae of Tropical Africa', Baker[20] states that it is hardly varietally distinct from *S. erecta*. Since there is no line of demarcation with reference to degree of pubescence among the specimens, it does not seem wise to retain either variety.

The inflorescence is usually much longer than broad, often becoming interrupted, although some specimens have more ovoid and compact heads. The leaflets in some specimens are punctate beneath.

[20] Legum. Trop. Afr. 320. 1926.

In addition to the localities listed, the species is reported to occur in Sierra Leone, Angola, and Gaboon. The habitats include dry gravelly hills, sea sands, sandy pastures, and sandy thickets along rivers.

BELGIAN CONGO: Leopoldville, from Boma to Shinkakasa, *Claessens s. n.* (GH).
FRENCH WEST AFRICA: IVORY COAST: Grand Drewin, *Roberty 13710* (MO). SENEGAL: exact locality unknown, *Sieber 37* (MO, NY).
GOLD COAST: Keta, *Darko 584* (MO); "Pram and Pram", *Robertson 32* (MO).
LIBERIA: exact locality unknown, *Cook 137, 145* (US).
NIGERIA: Lagos (Apapa), *Bels 43* (MO); exact locality unknown, *Vogel s. n.* (GH).

6. STYLOSANTHES SCABRA Vog. in Linnaea 12:69. 1838, ex char.

Stylosanthes diarthra Blake, in Proc. Biol. Soc. Wash. 33:49. 1920. (T: *Jahn 169*!)
Stylosanthes gloiodes Blake, loc. cit. 45. 1920. (T: *Townsend A 57*!)
Stylosanthes plicata Blake, loc. cit. 46. 1920. (T: *Kuntze s. n.*!)

Stems suffruticose, ascending to suberect, much branched, to 1.5 m. tall, densely and shortly hairy and often setosulous, sometimes viscid, rarely glabrescent. Leaflets elliptic to oblong-lanceolate, obtuse, mucronate, densely and shortly hairy above and below, sometimes glabrescent, with a few scattered setae, with 4–5 pairs of usually conspicuous veins; terminal leaflet to 15 mm. long, 5 mm. broad, the lateral ones to 12 mm. long and 4.5 mm. broad, often punctate beneath; petioles 2.5–6.0 mm. long, canaliculate above, scabrous with dense short hairs, the rhachis 1.0–3.5 mm. long; sheath and teeth of the stipules variable in length, the sheath usually 1.5–5.0 mm. longer than the teeth, short-hispid, 7- to 9-nerved. Spikes short, crowded, oblongoid, several-flowered; bracts unifoliolate, the leaflet about 4 mm. long, hispid, the sheath 3.5–6.5 mm. long, 3.0–4.5 mm. broad, densely hispid, about 7-nerved, the teeth 2.5–4.5 mm. long and somewhat shorter than the sheath; outer bracteole 1, lanceolate, 2.0–4.5 mm. long, bifid and ciliate at the apex; axis rudiment 4–5 mm. long, ciliate; inner bracteoles 2, 2–4 mm. long, ciliate at the apex. Calyx tube 3.0–6.5 mm. long, the more or less acute lobes 1.5–3.5 mm. long. Standard broadly obovate to suborbiculate, to 7 mm. long and 6 mm. broad; wings clawed, auriculate, spurred within at the base, 4–5 mm. long; keel petals auriculate, 3.5–4.5 mm. long. Loment about 2.5 mm. broad, reticulate-nerved; upper articulation 2–4 mm. long, shortly hairy, the lower 2–3 mm. long, evenly pilose throughout; beak uncinate, shortly hairy, 1–2 mm. long, one-half to one-third as long as the upper articulation.

The species has a wide range but is apparently most abundant in the Minas Geraes area of Brazil. It is attributed to Peru by Bentham[21] (fig. 4).

Stylosanthes scabra of § STYLOSANTHES is the viscid counterpart of *Stylosanthes viscosa* of § ASTYPOSANTHES.

BOLIVIA: LA PAZ: Larecaja, *Mandon 698* (GH).
BRAZIL: BAÍA: exact locality unknown, *Salzmann s. n.* (MO). MATO GROSSO: exact locality unknown, *Kuntze s. n.* (NY, US). MINAS GERAES: Ituiutaba, *Macedo 2226* (MO); Santa Luzia, *Williams & Assis 201* (GH, MO), *Barreto 5773* (F); Serro, *Williams*

[21] In Mart. Fl. Bras. 15^2:1. 1859.

& *Assis 6850* (GH, US). PARAÍBA: exact locality unknown, *de Moraes 887* (NY). PERNAMBUCO: Tapera, *Pickel 2556* (GH, US, NY, F), *2481* (GH, US, NY); Tiuma, *Millspaugh 67* (F); exact locality unknown, *Gardner 973* (GH, NY, US, F). RIO GRANDE DO SUL: Jacuí, *Téodoro 1783* (GH). SÃO PAULO: Campinas, *Santoro 638* (US); Avenida Barão Itapura, Campinas, *Santoro 380* (US); San José do Barreiro, *Hoehne & Gehrt 17665* (GH). WITHOUT PRECISE LOCALITY: São João Bapt., *Pohl 567* (NY).

COLOMBIA: CUNDINAMARCA: Aguadita, *Ricardo s. n.* (US). HUILA: between Hobo and Gigante, *Arbeláez & Cuatrecasas 8328* (US, F). EL VALLE: Cali, *Bermúdez 20* (US), *Killip & Cuatrecasas 38410* (US); Carretera al Mar, west of Cali, *Killip & Lehmann V 39798* (US); Cisneros, Dagua Valley, *Killip 11431* (US, GH, NY); north of Palestina, *Garcia 6328* (US); Trés Cruces, *Bermúdez & Barkley 17C869* (NY, US).

ECUADOR: Cariamanga, *Townsend A 57* (US).

VENEZUELA: MÉRIDA: Sierra de Nevada de Mérida, *Jahn 108* (US); above Los Gonzalez, *Steyermark 56234* (F). TRUJILLO: Valera, *Jahn 169* (US); Nagua, *Warming 101* (US).

7. STYLOSANTHES TUBERCULATA Blake, in Proc. Biol. Soc. Wash. 33:48. 1920. (T: *Britton 3336*!)

Stems suffruticose to 5 dm. tall, erect, branched, evenly and densely pilose and with dense short tuberculate-based hairs. Leaflets elliptic to oblong-lanceolate, acute and often mucronulate at the apex, the margins bristly-ciliate, both surfaces more or less appressed-pilose and often tuberculate-hispid at least below, with 4–6 pairs of prominent lateral nerves; terminal leaflet 10–20 mm. long, 3–5 mm. broad, the lateral ones somewhat smaller; petioles 2–4 mm. long, hispid-setose, the rhachis about 1 mm. long; sheath of the stipules 5–7 mm. long, pubescent and hispidulous as the stem, the subulate teeth 2–3 mm. long. Spikes narrowly oblongoid, 6–15 mm. long, 6- to 10-flowered; bracts unifoliolate, the leaflet pilosulous and densely tuberculate-hispid, the sheath 3.5–5.0 mm. long, hispidulous, the teeth slightly shorter; outer bracteole 1, 3–4 mm. long, bifid or entire, obtuse, ciliate or glabrous; axis rudiment 3–4 mm. long in fruit, pilose; inner bracteoles 2, 2–3 mm. long, narrow, ciliate or glabrous. Calyx tube 4–5 mm. long, glabrous, the obtuse lobes 2.5–3.0 mm. long, ciliate or glabrous. Standard 4–5 mm. long, 3–4 mm. broad; wings somewhat auriculate at the base, short-spurred within, 4–5 mm. long; keel petals falcate, 3.0–4.5 mm. long. Loment reticulate-nerved, about 2.5 mm. broad; upper articulation of the loment fertile, 3–4 mm. long, usually sparsely or occasionally densely pilosulous on the ribs, the lower articulation fertile or abortive; beak slightly uncinate, shortly hairy, at least near the base, 1.5–2.0 mm. long.

In savannas and on open banks at altitudes from 400 to 1800 meters (fig. 4).

BAHAMAS: NEW PROVIDENCE ISLAND: Southwest Landing, *Britton 3336* (US).

CUBA: CAMAGÜEY: Pueblo Romano, Cayo Romano, *Shafer 2463* (US, NY, F).

COLOMBIA: ANTIOQUIA: Medellín, *Archer 1002* (GH, US). CAUCA: La Paila, *Holton 22* (NY). HUILA: Quebrada de Angeles to Río Cabrera, *Rusby & Pennell 325* (NY); Gigante, Ancón, *Plata 72* (US). NORTE DE SANTANDER: Río Zulia, *Nicifaro s.n., 2412* (US). EL VALLE: Cali, *Fosberg 22001* (US); Dagua, *Killip 5431* (NY, GH, US); Jamundi, *Bermúdez 24* (US). WITHOUT PRECISE LOCALITY: Tocoima, *Arbeláez 2237* (US).

PERU: HUANCAVELICA: Tayacaja, below Colcabamba, valley of the Mantaro, *Weberbauer 6451* (GH, US, F).

VENEZUELA: DISTRITO FEDERAL: around Caracas, *Pittier 9754* (NY, US, GH). WITHOUT PRECISE LOCALITY: Avila, *Vogl 661* (F).

8. STYLOSANTHES SYMPODIALIS Taub. in Verh. Bot. Brand. 32:19. 1890. (T: *Spruce 6373*, photo!)

Stylosanthes psammophila Harms in Fedde, Rep. Sp. Nov. 19:69. 1923. (T: *Weberbauer 5936*!)

Stems erect, to 4.5 dm. tall, branched from near the base, shortly villous above, glabrate below, rarely with short bristles. Leaflets narrowly lanceolate to elliptic, acute at the tip, the larger ones to 40 mm. long and 5.5 mm. broad, evenly villous on both surfaces, usually with long marginal cilia, with 4–6 pairs of moderately conspicuous veins; petioles to 10 mm. long, usually much shorter, pilose, the rhachis about 2 mm. long; sheath of the stipules covered with soft short often rufous hairs, rarely with a few bristles. Spikes few-flowered; outer bracts usually trifoliolate, the inner unifoliolate, the sheath about 2 mm. longer than the teeth, densely covered with soft often rufous hairs, rarely with tuberculate bristles, 5- to 7-nerved; outer bracteole 1, 2.5–3.0 mm. long, pilose near the apex; axis rudiment to 7 mm. long, with long rufous hairs; inner bracteoles 2, 2.0–2.5 mm. long, pilose near the apex. Calyx tube 3–5 mm. long, the acute, ciliate lobes 1–2 mm. long. Standard about 4.5 mm. long, suborbiculate; wings 3–4 mm. long, auriculate at the base; keel petals 3–4 mm. long, auriculate. Loment strongly reticulate-nerved, to 2 mm. broad; both articulations of the loment usually fertile, the upper about 3 mm. long, glabrous below, with tawny hairs above, the lower nearly as long, densely pilose; beak 2.0–2.5 mm. long, usually slightly shorter than the upper articulation, uncinate or almost with a complete coil, densely covered with short hairs.

Occurs in sandy soils on the Galapagos Islands and in Peru and Ecuador. The specimens from the Galapagos Islands have leaflets 5–15 mm. long which sometimes bear short erect hairs along with the rufous pilosity on the bracteal sheaths. The continental specimens have longer and more narrow leaflets (to 40 mm. long) and usually possess only appressed pubescence on the bracteal sheaths. These latter specimens have been determined by some as S. *psammophila*.

In his monograph of *Stylosanthes*, Taubert describes under S. *scabra* an unnamed variety from the Galapagos Islands, stating "*var. caulibus villoso-pubescentibus, non scabris.*" These specimens belong to S. *sympodialis*.

ECUADOR: GALAPAGOS ISLANDS: Abingdon Island, *Snodgrass & Heller 836* (GH); Albemarle Island, Tagus Cove, *Stewart 1695* (MO, GH, US, NY), *Snodgrass & Heller 171* (GH), *Howell 9599* (GH); Bindloe Island, *Snodgrass & Heller 767* (GH), *Baur 90* (GH); Charles Island, *Snodgrass & Heller 450* (GH), *Stewart 1697* (MO, GH, US, NY), *Baur 92* (GH), Post Office Bay, *Howell 8815* (GH, US), Black Beach, *Svenson 151* (GH, F); James Island, *Rorud 144* (GH); Jervis Island, *Baur 89* (GH); North Indefatigable Island, *Snodgrass & Heller 673* (GH); Santa Cruz Island, *Rorud 145* (GH); South Seymour Island, *Howell 9948* (US). GUAYAS: Playas, *Asplund 5086* (US); Punta Carnero, *Svenson 11301* (NY); Salinas, *Svenson 11400* (US, GH); Punta Centinella, *Svenson 11258* (NY); Salinas, La Puntilla, *Asplund 5610* (US); Salinas, *Asplund 5650* (US). PIURA: exact locality unknown, *Eggers 14798* (US). WITHOUT PRECISE LOCALITY: *Espinosa 517, 590* (US).

Fig. 4

PERU: PIURA: Parinas Valley, *Haught 134* (US, NY); Negritos, *Haught F 44* (NY, F); between Piura and Nomala, *Weberbauer 5936* (GH, US). TUMBES: Zarumilla, *Ferreyra 5960* (US).

9. STYLOSANTHES **fruticosa** (Retz.) Mohlenbrock, comb. nov.

Hedysarum hamatum acc. Burm. f. Fl. Ind. 167. 1768, non L.
Arachis fruticosa Retz. Obs. Fasc. 5:26. 1791, ex char.
Stylosanthes mucronata Willd. Sp. Pl. 3:1166. 1800, ex char.
Stylosanthes bojeri Vog. in Linnaea 12: 68. 1838, ex char.
Stylosanthes aprica Span. in Linnaea 15:192. 1841, ex char. (T: *Burke & Zeyher 404*.)
Stylosanthes setosa Harv. in Harv. & Sond. Fl. Cap. 2:227. 1862, ex char.
Stylosanthes flavicans Baker in Oliv. Fl. Trop. Afr. 2:156. 1871. (T: *Kotschy 425*!)

Stem suffrutescent, about 5 dm. tall, much branched, erect or spreading, sometimes prostrate, shortly white-hairy above, occasionally with scattered short bristles, these sometimes yellow, often puberulent or glabrescent below. Leaflets acute,

rarely obtuse at the tip, glabrous or puberulent to densely short-hairy, often with scattered short setae on the margins and midvein beneath, with 3–4 pairs of conspicuous nerves, or with the veins rarely obscure; terminal leaflet to 17 mm. long (rarely to 25 mm. long) and 3.0–4.5 mm. broad (rarely to 8 mm. broad), the lateral to 16 mm. long and 3.0–4.5 mm. broad; petioles 4–7 mm. long, hispidulous or shortly bristly, sometimes puberulent, the rhachis 1.0–2.5 mm. long; sheath of the stipules 4.5–10.0 mm. long, densely and shortly hairy and usually with scattered bristles, or sometimes only with bristles, with 5–7 pairs of conspicuous nerves, the subulate teeth 3–6 mm. long, never longer than the sheath. Spikes ovate, dense, 4- to 10-flowered; bracts mostly unifoliolate, the leaflet(s) often plicate, the sheath tuberculate-bristly to merely long-ciliate around the margins, 3.0–6.5 mm. long, 2.5–5.5 mm. broad, about 7-nerved, the teeth averaging 3–5 mm. long, often nearly equaling the sheath; outer bracteole 1, 4–6 mm. long, ciliate at the apex; axis rudiment 3–5 mm. long, ciliate; inner bracteoles 2, 2.5–4.5 mm. long, ciliate at the apex. Calyx tube 4.5–6.5 mm. long, the lobes 2–4 mm. long, ciliate. Standard suborbiculate, 4.5–7.0 mm. long; wings 4–5 mm. long, auriculate at the base; keel petals 4–5 mm. long, auriculate. Loment 1.5–2.5 mm. broad, reticulate; both articulations usually fertile, or the lower sometimes abortive; lower articulation, when fertile, 2.5–4.0 mm. long and as long as or slightly longer than the upper, pilose; beak somewhat uncinate or scarcely coiled, 1.5–3.0 mm. long, shortly hairy.

The specimens of *Stylosanthes* from Africa and adjacent areas which belong to § STYLOSANTHES seem to be treated best as belonging to two highly variable species: S. *erecta* from West Tropical Africa, and S. *fruticosa* from South Africa, Madagascar, India, and Ceylon. The former has loments which are glabrous or nearly so, while S. *fruticosa* possesses pubescent loments.

Stylosanthes fruticosa is extremely diverse in its morphology, and a large number of variants have been described. In this study, the only course that seemed practical was to consider all these variants as belonging to one exceedingly broad species. The basis for the deluge of species seems to be mostly the pubescence of the stems, leaves, bracts, and stipules. In all of these, however, the loment characters remain essentially uniform. Thus S. *aprica* described from Timor, S. *bojeri* from Zanzibar, S. *flavicans* from Sudan, and S. *setosa* from the Cape are being treated as S. *fruticosa*. S. *sundaica* of Malaysia, considered by most recent authors as a synonym for S. *fruticosa*, is really a synonym for a species in § ASTYPOSANTHES

Specimens collected in Kordofan by Pappi (*364*) and by Kotschy (*425*) are the basis for Baker's S. *flavicans*. These specimens are flavescent when dried and somewhat viscid and apparently represent an extreme in the S. *fruticosa* complex. Many of the bristly specimens of S. *fruticosa* are at least subviscid, however, and no dividing line may be drawn to separate the specimens. Specimens called S. *bojeri* are very bristly and are sordid upon drying. This again seems to represent only an extreme, and intergradations of all degrees of pubescence may be found.

Apparently the first mention of this species in the literature was in 1737 when

Burmann[22] recorded the polynomial '*Trifolium procumbens zeylanicum hirsutum.*' In 1768 Burmann f.[23] noted that *Hedysarum hamatum* occurred in Ceylon and Jamaica. It is evident that he included under this binomial at least two species, the present *S. hamata* (L.) Taub. from Jamaica which Linnaeus called *Hedysarum hamatum α* in 1759 and *S. fruticosa* from Ceylon. In 1791 Retzius[24] named *Arachis fruticosa* from Ceylon and included under it Linnaeus' *Hedysarum hamatum α*. Nine years later, Willdenow[25] described *S. mucronata* and listed *Arachis fruticosa* as a synonym. Therefore it appears that the first legitimate epithet to be applied to this species is *fruticosa.*

KENYA: trail from Nyeri to Wambugu, *Mearns 1956* (NY, US); 14 miles from Mombassa, vicinity of Changamme, *Mearns 2230* (US).

MOZAMBIQUE: Lourenço Marques, *Howard 56* (US), *Barle 82* (US), *Curtis 80* (GH); Lourenço Marques, Marracuene, *Quintas 6* (MO); Delagoa Bay, *Kuntze s. n.* (NY); Maputo, *Sousa 3960* (MO).

NIGERIA: on the Niger, *Baikie s. n.* (GH); exact locality unknown, *Barter 3428* (GH).

SOUTHERN RHODESIA: Matapos, *Plowes 1426* (MO); Nyamandhlovu, Plowes *1603* (MO); Umtali, *Chase 3231* (NY).

SUDAN: KORDOFAN: Nile Land, *Kotschy 425* (GH).

TANGANYIKA: Ugogo, Dodoma, *Peter 44443, 44463* (MO); Nzega, 50 miles north of Tabora, *Carnochan 10* (GH); near Manyoni, north of Kilimatinbe, *Carnochan 338* (GH); Dar-es-Salaam, *Kuntze s. n.* (NY).

UNION OF SOUTH AFRICA: TRANSVAAL: Barberton, *Thorncroft 1913* (NY); near Crocodile Poont, *Dyer & Verdoorn 3426* (NY); Pretoria, *Mogg 14785* (US). ZULULAND: Somkele, *Wood 9291* (US).

CEYLON: exact locality unknown, *Thwaites 1451* (GH, NY).

EAST INDIES: exact locality unknown, *Wight 814* (NY).

INDIA: Mysore and Carnatic, *Thompson s. n.* (GH); Salem, Hosur, *Yeshoda 415* (NY).

10. STYLOSANTHES SUBSERICEA Blake, in Proc. Biol. Soc. Wash. 33:50. 1920. (T: *Purpus 7152*!)

Stylosanthes scoparia Standl. & L. Wms. in Ceiba 1:145. 1950. (T: *Williams & Molina 11261*!)

Stems suffruticose, usually erect, slender to robust, to 1 m. tall, often much branched, long-pilose and usually sericeous throughout, occasionally with a few bristles near the inflorescence, sometimes glabrescent. Leaves crowded, the leaflets lanceolate, acuminate, the terminal to 20 mm. long and 4.5 mm. broad, the lateral to 15 mm. long and 3.5 mm. broad, shortly white-hairy on both surfaces with occasional bristles below, with 3–5 pairs of conspicuous veins often forming a submarginal nerve; petioles 5–7 mm. long, densely white-hairy, the rhachis 1.5–2.0 mm. long, pubescent as the petioles; sheath of the stipules 5–9 mm. long, sericeous with occasional scattered tuberculate-based bristles, 9- to many-nerved, the teeth lance-subulate, 6.0–7.5 mm. long. Spikes narrow, oblongoid, 4- to 10-flowered, 12–20 mm. long, on peduncles 0.5–4.0 mm. long; bracts unifoliolate, often short-

[22] Burmann, Thes. Zeyl. 1737.
[23] Burmann f., Fl. Ind. 167. 1768.
[24] Retz. Obs. Bot. Fasc. 5:26. 1791.
[25] Willd. Sp. Pl. 3:1166. 1800.

bristly on the back, 4.0–5.5 mm. wide, the sheath 4.0–5.5 mm. long and 7- to 9-nerved, the teeth 3.5–5.0 mm. long; outer bracteole 1, 4–7 mm. long, pilose nearly throughout; axis rudiment about 6 mm. long in fruit, long-ciliate; inner bracteoles 2, 3–4 mm. long, ciliate. Calyx tube 6–8 mm. long, the lobes 3–5 mm. long, the upper two lobes obtuse and long-pilose, the lateral ones similar but somewhat shorter, the lowest acute, pilose. Standard suborbiculate, 5–8 mm. long; wings mostly obovate and with a short claw, auriculate, shortly spurred, 4–6 mm. long; keel petals 3.5–5.0 mm. long, spurred within at the base. Loment about 2.5 mm. wide, conspicuously reticulate; both articulations usually fertile, the lower 3–4 mm. long and densely long-pilose, the upper 3.5–4.0 mm. long, sometimes slightly exceeding, sometimes slightly shorter than the lower, covered with long white hairs; beak 2.5–5.0 (–7.0) mm. long, white-hairy, with a distinct coil.

Stylosanthes subsericea is the woodiest member of the genus and sometimes attains a height of one meter. The circinate beak of the pubescent loment nearly equals or surpasses the upper articulation in length. The lower leaves fall early, leaving the stem bearing only the persistent subulate stipules near the base.

All the Honduran specimens previously have gone under the binomial S. *scoparia*. However, the great similarity of floral structure and vegetative characters of the Honduran plants with S. *subsericea* of Mexico indicates these two epithets to refer to the same species. The Mexican plants lack tuberculate bristles on the lower surface of the leaflets.

The species is very local and is known only through a few collections from Honduras and Oaxaca, Mexico, where it grows in regions of dry rocky hillsides and dry ravines, usually with pines and oaks, at elevations between 600–850 meters.

HONDURAS: COMAYAGUA: vicinity of Comayagua, *Standley & Chacon 5866* (F), *5400* (F). MORAZÁN: Río Yeguare, near El Zamorano, *Standley & Molina 4631* (F); Quebrada de Santa Clara, near Río Yeguare, *Standley & Williams 1598* (F); above El Zamorano, between Jicarito and El Pedregal, *Standley 12260* (F); along Río Yeguare, east of El Zamorano, *Standley 14593* (F); San Francisco, *Williams & Molina 13220* (F); Tatumbla, *Rodríguez 509* (F); Santa Inés, *Rodríguez 478* (F); Río Yeguare, *Rodríguez 973* (F); Las Mesas, *Standley 21222* (F); Quebrada de Santa Clara, *Standley & Williams 1563* (F); above El Jicarito, *Standley 21112* (F); Río Yeguare valley, Santa Clara Creek, *Williams & Molina 11261* (GH, F); near Las Mesas, *Standley 28654* (US); Río Yeguare, between Tatascan and Maraíta, *Molina 4079* (US); Camino Viejo between Suyapa and Tegucigalpa, *Standley 14213* (US, F); near Río Yeguare, below El Zamorano, *Standley 12110* (MO, F); Río Capa Rosa, El Zamorano, *Rodríguez 3662* (US, F); Quebrada de Santa Clara, near Río Yeguare, *Standley & Williams 1634* (US, F); along Río Yeguare, east of El Zamorano, *Standley 1077* (US, F). EL PARAÍSO: Quebrada de Dantas, on road between Las Mesas and Yuscarán, *Standley 14983* (MO, F); vicinity of Güinope, *Standley, Williams, Molina & Padilla 2077* (F); south of Güinope, *Standley 14862* (F); Río Yeguare, *Molina 1681* (F); Caleras, *Williams & Molina 14133* (F).

MEXICO: OAXACA: Cerro de Picacho, *Purpus 7152* (GH, NY, US, MO, F); near Oaxaca, *Rose & Hough 4584* (US).

Fig. 5

11. Stylosanthes macrocarpa Blake, in Proc. Biol. Soc. Wash. 33:47. 1920. (T: *Pringle 6721*!)

Stems herbaceous throughout, much branched from the base, spreading or ascending, to 20 cm. tall, densely covered with mostly appressed-ascending pili, with short tuberculate bristles beneath each node. Leaflets elliptic, subacute, mucronate, light green, glabrous above, sparsely bristly on the midvein beneath and along the margins, with 3–4 pairs of conspicuous veins; terminal leaflet to 13 mm. long and 3.5 mm. broad; petioles 3–5 mm. long, sparsely pilose and often shortly bristly, the rhachis 1.0–2.5 mm. long; sheath of the stipules about equaling the teeth, 3–4 mm. long, pubescent like the stem. Spikes ovoid, to 15 mm. long, 5- to 10-flowered; outer bracts trifoliolate, the inner unifoliolate, the sheath pilose and bristly, 6–8

mm. long, about twice as long as the teeth, 7-nerved; outer bracteole 1, oblong, about 4.5 mm. long, ciliate near the apex; axis rudiment to 8 mm. long in fruit, long-hairy; inner bracteoles 2, 2.5–3.0 mm. long. Calyx tube 5–6 mm. long, the obtuse lobes 2–3 mm. long. Standard obovate, not clawed, about 6 mm. long; wings auriculate below and shortly appendaged within; keel petals falcate. Loment 6.0–8.5 mm. long, 3.0–3.5 mm. broad, reticulate; usually only the upper articulation fertile, 4.0–4.5 mm. long, evenly appressed-pilosulous, the lower abortive or occasionally fertile, densely pilose; beak strongly uncinate, evenly appressed-pilosulous, 3.5–4.0 mm. long, usually equaling the superior articulation.

Stylosanthes macrocarpa, known only from hills near Oaxaca, Mexico, closely resembles S. *mexicana* but differs in fruit morphology. The loment of S. *macrocarpa* is evenly appressed-pilosulous throughout while that of S. *mexicana* is glabrous or puberulent only along the nerves.

The flowers examined show two inner bracteoles although Blake,[26] in his original description, states the number of "bractlets" (= inner bracteoles) to be 1, a character not in keeping with the other members of § STYLOSANTHES. One of the large sub-basifixed anthers in some of the flowers is about twice as large as the other four. This seems to be only a sporadic anomaly.

MEXICO: OAXACA: near Oaxaca, *Pringle 5782* (GH); Monte Albán, *Pringle 372* (GH).

12. STYLOSANTHES NERVOSA Macbr. Field Mus. Publ. Bot. 13^3:411. 1943. (T: *Weberbauer 6215*!)

Stems suffrutescent, to 1 m. tall, erect, branched, usually villous with interspersed tuberculate-based hairs, at least when young. Leaflets oblong-lanceolate, acute to acuminate, glabrous or nearly so above, puberulent beneath with occasional tuberculate hairs (at least on the costa), with 4–6 pairs of conspicuous nerves, the terminal leaflet to 20 mm. long and 3 mm. broad, the lateral somewhat smaller; petioles 2–4 mm. long, pilose with occasional tuberculate hairs, rarely glabrous, the rhachis about 1 mm. long; sheath of the stipules about 7 mm. long, usually equaled by the subulate teeth, pilose, glabrate, with 5–7 nerves. Spikes narrowly oblong-lanceolate, 2- to 8-flowered; bracts unifoliolate, the leaflet ciliate, the sheath 5–7 mm. long, with numerous tuberculate hairs, densely ciliate, 5- to 7-nerved, the teeth usually 3–5 mm. long, sometimes bearing tubercles; outer bracteole 1, 4–5 (–7) mm. long, ciliate at the apex; axis rudiment 3–4 mm. long, ciliate; inner bracteoles 2, 3–4 mm. long, ciliate at the apex. Calyx tube about 7 mm. long, the lobes 3 mm. long, the upper 4 obtuse, ciliate or glabrous. Standard 5–6 mm. long; wings somewhat auriculate at the base, shortly spurred within; keel petals 3.5–5.0 mm. long, falcate. Loment about 2 mm. broad, reticulate; only the upper articulation usually fertile, about 3.5 mm. long, evenly pilose throughout; beak about 2.5 mm. long, pilose, strongly uncinate but usually not completely coiled.

[26] In Proc. Biol. Soc. Wash. 33:47. 1920.

Infrequent over a broad range, known only from a few stations in Venezuela, Peru, Bolivia, and northern Argentina (fig. 4).

ARGENTINA: CORRIENTES: exact locality unknown, *Ibarrola 2310* (US). SALTA: La Merced, *Venturi 5136* (GH, US).
BOLIVIA: SANTA CRUZ: Buena Vista, *Steinbach 5397* (NY, GH).
PERU: CAJAMARCA: Jaen, near mouth of Chinchipe River, *Weberbauer 6215* (NY, GH, US, F).
VENEZUELA: Serranias de Terepaima, *Saer 631* (F).

13. STYLOSANTHES HAMATA (L.) Taub. Verh. Bot. Brand. 32:22. 1890.

Hedysarum hamatum α L. Syst. Nat. 10:1170. 1759, ex char.
Stylosanthes procumbens Sw. Prod. Veg. Ind. Occ. 108. 1788, ex char.
Stylosanthes humilis Rich. ex Hemsl. in synon., Biol. Centr. Am. Bot. 1:272. 1882, ex char.
Stylosanthes eriocarpa Blake, Contrib. U. S. Nat. Herb. 24:4. 1922. (T: *Blake 7792*!)

Stems ascending, spreading, prostrate, or matted, to 1 m. tall, often much branched, usually with a line of fine pubescence on one side of the stem, sometimes glabrous near the base or rarely throughout, or occasionally sericeous throughout. Leaflets lanceolate to elliptic, obtuse to subacute, to 20 mm. long and 6 mm. broad, glabrous or shortly pilose above and below, with 3–6 pairs of conspicuous veins; petioles 2–6 mm. long, puberulent or pilose, the rhachis 0.5–2.5 mm. long; sheath of the stipules shortly hairy, sericeous, or glabrous, 3- to 11-nerved, usually exceeding or occasionally surpassed in length by the teeth. Spikes rather small, ovoid to oblongoid, few- to 15-flowered; outer bracts trifoliolate, inner usually unifoliolate, very variable in pubescence of the sheath, mostly only ciliate, the sheath 5- to 7-nerved; outer bracteole 1, 2.5–5.0 mm. long, ciliate at the apex; axis rudiment 2–7 mm. long; inner bracteoles 2, 2.5–3.5 mm. long, ciliate at the apex. Calyx tube 4.0–7.5 mm. long, at least twice as long as the more or less acute and ciliate lobes. Standard 4–5 mm. long, suborbiculate; wings 3.5–4.5 mm. long, clawed and auriculate; keel petals 3.0–4.5 mm. long, falcate. Loment about 2 mm. broad, reticulate; both articulations usually fertile, the upper 2–4 mm. long, glabrous or puberulent in localized areas, or densely and evenly sericeous, the lower, when fertile, somewhat shorter, pilose or glabrescent; beak equaling to exceeding the upper articulation, glabrous or with short pubescence, uncinate.

Stylosanthes hamata is readily distinguished by a series of characters which includes a more or less puberulent bi-articulate loment with a beak slightly exceeding the upper articulation and a general lack of tuberculate bristles.

This species appears to be related most nearly to *S. fruticosa* of Africa and, indeed, the two were not separated by such early authors as Burmann f. and Retzius. *Stylosanthes fruticosa* usually possesses tuberculate bristles and evenly pilosulous loments. *Stylosanthes hamata* is similar to *S. sympodialis* but in the latter the beak of the loment is shorter than the upper articulation.

The spikes are usually 2- to 5-flowered, but some specimens from the Antilles have large dense spikes which may bear as many as 15 flowers. The habit of this species may be erect to ascending, or prostrate and matted. This difference seems

to be correlated with altitude; the specimens from elevations between 100 and 900 meters tend to be upright while those near sea level seem to be matted. These latter have been known as S. *procumbens.*

The range of S. *hamata* is broad and includes Florida, eastern Mexico and Central America, the Antilles, Colombia, and Venezuela, often becoming a pest in gardens in Jamaica, Cuba, and neighboring islands.

UNITED STATES: FLORIDA: Dade Co.: *Moldenke 778* (MO).

BAHAMAS: ANDROS ISLAND: Spaniard Creek, *Small & Carter 8882* (F, NY, GH, US); Mastic Point, *Brace 7097* (NY, F); road to Little Creek, *Brace 5245* (NY). CAICOS ISLANDS: South Caicos, *Wilson 7637* (GH, NY, F); Jacksonville, *Millspaugh & Millspaugh 9100* (NY, F). CROOKED ISLAND: Marine View Hill, *Brace 4635* (NY, F); Landrail Point, *Brace 4678* (NY, F). ELEUTHERA ISLAND: Current, *Coker 339* (NY). GRAND BAHAMA ISLAND: Eight Mile Rocks, *Britton & Millspaugh 2454* (GH, NY, US, F). GRAND TURK ISLAND: The Wells, *Millspaugh & Millspaugh 9342* (NY, US, F); Waterloo, *Millspaugh & Millspaugh 9034* (F). GREAT RAGGED ISLAND: exact locality unknown, *Wilson 7821* (GH, NY, F). NEW PROVIDENCE ISLAND: Nassau, *Hitchcock s. n.* (MO, F); Clifton Point, *Degener 18985* (GH, NY, MO); Nassau, *Northrop & Northrop 37* (GH, NY, F), *Curtiss 9, 118* (GH, US, NY, MO, F), *Coker 541* (NY), near Fort Fincastle, *Wright 86* (GH, NY, F), off Soldier's Road, *Wright 223* (GH, NY), road to Lake Cunningham, *Britton 93* (NY), west of Bay Street Road, *Millspaugh 2172* (F); exact locality unknown, *Brace 444* (F). RUM CAY: Port Nelson, *Brace 3934* (NY, F). SAN SALVADOR ISLAND: exact locality unknown, *Wilson 7359* (NY, F).

CUBA: CAMAGÜEY: Pueblo Romano, Cayo Romano, *Shafer 2499* (NY). HABANA: Habana, *Palmer & Riley 821* (US), *Babs 460* (NY); Regla, *Shafer 104*; Playa de Cojimar, *Hitchcock s. n.* (F); Marianão, *Piper 6089* (US). ORIENTE: Santiago, Morro Hill, *Millspaugh 1077* (US, F), *Howard 5788* (GH, US, NY, MO); Guantánamo Bay, *Britton 1941* (US, NY); Holguin to Cacocum, *Shafer 1551* (US, NY); Santiago, *Havard 105* (NY); Santiago, Morro Castle, *Havard 82* (NY); Santiago, *Underwood & Earle 1682* (NY). WITHOUT PRECISE LOCALITY: Triscornia, *Hitchcock s. n.* (F).

DOMINICAN REPUBLIC: BARAHONA: Los Patos, *Abbott 1767* (US); Barahona, *Howard & Howard 8413* (GH, NY), *Fuertes 211* (GH, MO, NY, US, F), *von Türckheim 2804* (NY). SAN JUAN; near San Juan de la Maguana, *Howard & Howard 8795* (GH); El Cercado, Juan Santiago, Hondo, *Howard & Howard 9293* (NY). SANTIAGO: Santiago, *Jiménez 473* (US). SANTO DOMINGO: Monción, banks of Río Mao, *Valeur 802* (US); Guayubin, *Abbott 937a* (US), *942* (US); near Puerto Liberatador, Manzanillo Bay, *Howard & Howard 9659* (NY); Monción, *Valeur 248* (NY, US, MO, F); Ciudad Trujillo, *Allard 14350* (US), *13087* (US, F), *13114* (US), *13107* (US), *13313* (US), *13725* (US, MO), *14007* (US), *14281* (US); Azua, *Rose, Fitch & Russell 4028* (US, NY). WITHOUT PRECISE LOCALITY: Moca, *Ekman NH 11270* (US); Haina, *Faris 38* (US, NY); Llanos de Rafael, *Eggers 1920* (NY, US); Constanza, *von Türckheim 2529* (NY).

GRAND CAYMAN: South Sound, *Kings GC 69* (MO); Bodden Bay road, *Millspaugh 1335* (F).

HAITI: ARTIBONITE: vicinity of Ennery, *Leonard 8798* (GH, US, NY, MO), *8797* (F), *9463* (US); Gros Morne, *Leonard 9858* (US); St. Marc, *Leonard 2863* (US), *2881* (US). GONAIVES: Gonaives to La Hotte Rochée on road to Terre Neuve, *Nash & Taylor 1545* (NY). GONAVE ISLAND: Étroit, *Leonard 3401* (GH, US). MIREBALAIS: exact locality unknown, *Cook, Scofield & Doyle 81* (US). DU NORD: St. Michel de l'Atalaye, *Leonard 7037* (US); Plaisance to Marmelade, *Nash 678* (NY). NORD-OUEST: Jean-Rabel, *Leonard & Leonard 12925* (US); Port-de-Paix, *Leonard & Leonard 11001* (GH, US); vicinity of Bombardopolis, *Leonard & Leonard 13448* (NY, US). SUD: west of Jérémie, *Holdridge 928* (US). LA VALLÉE: Tortuga Island, *Leonard & Leonard 11224* (US, MO), *15583* (US). WITHOUT PRECISE LOCALITY: Plaine Centrale, Pavane-Papaye, *Ekman H6013* (US); La Cumbre, *Raunkaier 1137* (US).

Jamaica: Sherwood Forest, *Orcutt 3137* (MO); Port Morant, *Hitchcock s. n.* (MO); Kingston, *Hitchcock s. n.* (MO); near Port Antonio, *Fredholm 3054* (US, NY); Trelawny, Jackson Town, *Hunnewell 19781* (GH); Waterloo Road, *Campbell 6019* (NY); vicinity of Mandeville, *Brown 107* (NY).

Lesser Antilles: anegada: exact locality unknown, *Britton & Fishlock 1007* (US, NY, F). anguilla: exact locality unknown, *Boldingh 5536* (NY). antigua: St. Johns, *Shafer 36* (NY); exact locality unknown, *Hutson s. n.* (US). barbados: Waterford, St. Michael, *Dash 281* (US, NY, F); Codrington, *Borrell 281* (US); Hastings, *Waby 62* (US). bonaire: exact locality unknown, *Boldingh 7246* (NY). curaçao: Santa Cruz, *Britton & Shafer 3013* (NY). grenada: Richmond Hill, *Broadway s. n.* (US, NY). guadeloupe: Pointe-à-Pitre, *Hammarlund 18* (NY); exact locality unknown, *Questel 1459* (US). inagua: Salt Pond Hill, *Fairchild 2599* (US); Matthew Town, *Nash & Taylor 1069* (NY, F). mona: exact locality unknown, *Stevens 6224* (NY), *6344* (NY). st. barthélemy: Gustavia, *Questel 116* (NY), *217* (NY); exact locality unknown, *Forsström s. n.* (F). st. croix: Corn Hill, *Ricksecker 216* (GH, MO, NY, US, F); Judith's Ferry, *Thompson 482* (GH, NY); Bassin, *Ricksecker 47* (US, MO, F). st. jan: Bethania to Rosenberg, *Shafer 232* (US, NY). st. kitts: near Basseterre, *Britton & Cowell 729* (US, NY). st. thomas: Svenson's Bay, *Britton 280* (NY); Paradise Bay, *Britton & Britton 208* (US, NY). tortola: Sea Cow Bay, *Britton & Shafer 667* (GH, NY). virgin gorda: exact locality unknown, *Fishlock 163* (GH, NY).

Little Cayman: South Side, Blossom Point, *Kings LC 75* (MO).

Puerto Rico: Quebradillas, *Stevenson 5887* (US); Guanica, *Sintenis 3756* (NY, US); Yauco, *Underwood & Griggs 658* (US, NY); Guayama, Pozuelo, *Goll 531* (US); Cayey, south of Caguas, *Heller & Heller 328* (US, NY, F); Bayamon, *Sintenis 1092* (US, MO, NY); Condado, *Britton, Britton & Brown 5764* (US, NY).

Guatemala: izabal: trail from Los Amates to Izabal, *Blake 7792* (GH, US); Puerto Barrios, *Standley 25126* (NY, US).

Panama: coclé: Penonomé, *Shafer 36* (NY).

Colombia: atlántico: Salgar, around Puerto Colómbia, *de Kattah, Molina & Barkley At025* (US), *At048* (US); Barranquilla, *Elias 927* (US); Puerto Colombia, *Dugand 4008* (US). bolívar: La Popa, *Killip & Smith 14067* (NY, GH, US, F); Cartegena, *Molina & Barkley Bo048* (US). cundinamarca: east of Apulo, *Killip, Dugand & Jaramillo 38164* (US). magdalena: exact locality unknown, *Castañeda 252* (MO). tolima: Curvas de Gualanday, *Arbeláez & Cuatrecasas 6506* (US).

Venezuela: falcón: Adicora, Paraguaná, *Tomayo 750* (US), *977* (US, F). nueva esparta: Island of Margarita, *Miller & Johnston 68* (GH, NY, US, MO, F).

14. Stylosanthes sericeiceps Blake, in Contrib. U. S. Nat. Herb. 20:524. 1924. (T: *Jahn 678*!)

Stems suffruticose, erect, to 0.5 m. tall, densely covered with shortly appressed silvery hairs, glabrescent below. Leaflets lanceolate, to 25 mm. long and 5 mm. broad, acuminate, mucronate, usually glabrous above, minutely pubescent beneath and along the margins, with 4–7 pairs of prominent veins; petioles to 6 mm. long, sericeous, the rhachis to 2.5 mm. long; sheath of the stipules about as long as the teeth, densely short-hairy, with 3 veins crowded near the center. Spikes oblongoid or obovoid, about 15 mm. long, crowded, several-flowered; outer bracts often trifoliolate, inner unifoliolate, the sheath 5–7 mm. long, about equaling the teeth, densely covered with long tawny hairs, 5-nerved; outer bracteole 1, bifid, ciliate, about 4 mm. long; axis rudiment to 4 mm. long, densely pilose; inner bracteole 1, about equal in length to the outer but narrower. Calyx tube to 7 mm. long, the more or less pilose lobes obtuse or acute, about 3 mm. long. Standard to 8 mm. long, suborbiculate; wings 4.5–6.5 mm. long, auriculate; keel petals 4.5–6.0 mm. long, falcate. Loment 1.5–2.0 mm. broad, reticulate; both articulations fertile or

the lower sometimes abortive, the upper 2.5–3.0 mm. long, evenly clothed with short silvery hairs, the lower, when fertile, nearly 4 mm. long, pilose; beak 1.5–2.0 mm. long, nearly half as long as the upper articulation, strongly uncinate, densely white-hairy.

Stylosanthes sericeiceps apparently marks the transition between § STYLOSANTHES and § ASTYPOSANTHES in that only the lowest 2–3 flowers in each spike possess an axis rudiment and that each flower, in addition, is subtended by only one inner bracteole, the latter character one which is found throughout § ASTYPOSANTHES. The absence of the axis rudiment in upper flowers has been noted for some specimens in other species of § STYLOSANTHES (*S. hamata* and *S. subsericea*), but this is the only species in which this is combined with the absence of one of the inner bracteoles.

Stylosanthes sympodialis closely resembles S. *sericeiceps*, differing from it in the rufous villosity of the bracteal sheaths and in the unevenly pubescent loment.

There are no data as to the habitat of this species, except that it grows at altitudes between 400 and 1000 meters. It is known only from Venezuela.

VENEZUELA: MÉRIDA: Lagunillas, *Jahn 678* (US, GH, NY); between Estangues and Pointe Real, *Pittier 12842* (NY, US).

Section II. ASTYPOSANTHES (Herter) Mohlenbrock, stat. nov.

Sect. *Eustylosanthes* Vog. in Linnaea 12:63. 1838.
Astyposanthes Herter, in Rev. Sudamer Bot. 7:209. 1943.

None of the flowers subtended by an axis rudiment; inner bracteole 1.

In the absence of previous typification, *Stylosanthes humilis* HBK. is designated as the type for § ASTYPOSANTHES.

15. STYLOSANTHES BIFLORA (L.) BSP. Prelim. Cat. N. Y. Pl. 118. 1883.

Trifolium biflorum L. Sp. Pl. 773. 1753, ex char.
Arachis aprica Walt. Fl. Carol. 183. 1788, ex char.
Stylosanthes elatior Sw. in Svenska Vet. Akad. Handl. 11:296. 1789, ex char.
Stylosanthes hispida Michx. Fl. Bor. Am. 2:75. 1803, ex char.
Stylosanthes hispida var. *hispidissima* Michx. loc. cit. 1803, ex char.
Stylosanthes hispida var. *nudiuscula* Michx. loc. cit. 1803, ex char.
Stylosanthes hispida α erecta Pursh, Fl. Am. Sept. 2:480. 1814, ex char.
Stylosanthes hispida β procumbens Pursh, loc. cit. 1814, ex char.
Stylosanthes elatior β hispidissima Torr. & Gray, Fl. N. Am. 1:354. 1838, ex char. (T: *Michaux s. n.*)
Stylosanthes biflora α elatior O. Ktze. Rev. Gen. 1:209. 1891, ex char.
Stylosanthes biflora β guianensis O. Ktze. loc. cit. 1891, ex char.
Stylosanthes riparia Kearney, in Bull. Torr. Bot. Club 24:565. 1897. (T: *Kearney 674!*)
Stylosanthes biflora var. *hispidissima* Poll. & Ball, in Proc. Biol. Soc. Wash. 13:134. 1900, ex char.
Stylosanthes biflora var. *hispidissima* Mohr, in Contrib. U. S. Nat. Herb. 6:570. 1901, ex char.
Stylosanthes floridana Blake, in Proc. Biol. Soc. Wash. 33:51. 1920. (T: *Sudworth s. n.!*)
Stylosanthes riparia var. *setifera* Fern. in Rhodora 40: 438. 1938. (T: *Fernald & Long 8321!*)
Stylosanthes riparia f. *ochroleuca* Fern. loc. cit. 1938. (T: *Fernald & Long 8732!*)

Stems herbaceous to subligneous at the base, to 6 dm. tall, erect or spreading, much branched or rarely sparsely branched, glabrous to puberulent to densely hispid, the bristles sometimes yellowish. Leaflets ovate to elliptic to lanceolate, obtuse to acute at the tip, glabrous on both surfaces and occasionally with spinulose teeth on the margins, sometimes punctate beneath, with 3–6 pairs of nerves; terminal leaflet to 40 mm. long and 10 mm. broad, usually much smaller, the lateral ones slightly smaller than the terminal; petioles 1–3 mm. long, glabrous to puberulent to hispidulous, the rhachis 0.5–1.5 mm. long; sheath of the stipules 3–10 mm. long, glabrous to puberulent to densely hispid, with numerous nerves, the subulate teeth 3–8 mm. long, often setose. Spikes small, 1- to 8-flowered; bracts mostly unifoliolate or the outer sometimes trifoliolate, the sheath puberulent to densely hispid, rarely glabrous, 3.0–6.5 mm. long, 2.5–5.5 mm. broad, mostly 5- to 9-nerved, the teeth usually somewhat shorter; outer bracteole 1, lanceolate, 2–3 mm. long, glabrous to ciliate at the apex; axis rudiment none; inner bracteole 1, 1.0–2.5 mm. long, glabrous to ciliate at the apex. Calyx tube 2.5–5.0 mm. long, glabrous, the more or less acute lobes 2–4 mm. long, glabrous to puberulent. Standard suborbiculate, 4.5–7.0 mm. long, to 5.5 mm. broad; wings 3.5–4.5 mm. long, auriculate, spurred within at the base; keel petals denticulate to entire at the apex, auriculate, spurred within at the base. Loment 2.5–3.0 mm. broad, strongly reticulate with vertical nerves; only the upper articulation of the loment fertile, 2.5–5.0 mm. long, obovoid, plump, puberulent throughout; beak 0.5–1.0 mm. long, coiled.

The *Stylosanthes biflora* complex is defined as including populations not only of S. *biflora* but also S. *riparia* and S. *floridana* of other authors. The members of this complex are relatively constant with respect to loment characters but are diverse in leaflet shape, pubescence, and to some extent habit. However, some variation may occur in shape of the loments with some articulations more inflated than others, or in degree of reticulation. Loments are generally puberulent although they may become glabrous with age. Degree of maturity affects such characters of the loment so that in some specimens, the entire range of variability may be observed.

Most authors refer specimens with acute leaflets and without bristles on the stem to S. *biflora* (L.) BSP., and those with acute leaflets and bristles on the stem and bracteal sheaths to S. *biflora* var. *hispidissima* (Michx.) Pollard & Ball. Specimens with obtuse leaflets and which may be either non-bristly or bristly are regarded mostly as S. *riparia* Kearney or its variety *setifera* Fern., respectively. Specimens from the extreme southeastern United States which lack bristles completely are known sometimes as S. *floridana* Blake. A sharp line of demarcation among these variants is, however, difficult to determine, a fact which has been noted previously by some workers (Isely[27]).

Supposedly the best criterion to separate S. *riparia* from S. *biflora* is the position of the beak on the upper articulation of the loment. In S. *riparia*, the beak is said to

[27] Iowa State Coll. Jour. Sci. 30:113. 1955.

be oriented terminally on the loment rather than at one side as in *S. biflora*. However, in most specimens identified as *S. riparia*, the beaks appear lateral. Isely attributes the differences between fruits to "artifacts of observation" since "the degree to which the beak is or is not symmetrically placed may depend on the angle from which it is viewed".

Other varieties or species which have been segregated from *S. biflora* seem only to represent extremes.

United States:

Alabama: DeKalb Co.: *Ruth 338* (MO). Lee Co.: *Baker s. n.* (MO). Marshall Co.: *Hubricht B 1667* (MO). Mobile Co.: *Graves 961* (MO).

Arkansas: Baxter Co.: *E. J. Palmer 5961* (MO). Clark Co.: *Demaree 17794* (MO). Craighead Co.: *Demaree 3495* (MO). Cross Co.: *Demaree 19618* (MO). Dallas Co.: *Demaree 23350* (MO), *23340* (MO). Drew Co.: *Demaree 18016* (MO). Franklin Co.: *Demaree 17788* (MO). Hot Springs Co.: *Demaree 17463* (MO). Jefferson Co.: *Demaree 19460* (MO). Johnson Co.: *Demaree 19966* (MO). Lincoln Co.: *Demaree 19156* (MO). Logan Co.: *Demaree 17682* (MO). Miller Co.: *Heller & Heller 4126* (MO). Prairie Co.: *Demaree 22303* (MO). Pulaski Co.: *Demaree 17293* (MO). Saline Co.: *Demaree 21195* (MO). Sharp Co.: *Emig 168* (MO). Union Co.: *Demaree 19421* (MO). Yell Co.: *Demaree 21270* (MO).

Delaware: Newcastle Co.: *Commons s. n.* (MO). Sussex Co.: *Churchill s. n.* (MO).

Florida: Duval Co.: *Curtiss 6418* (MO). Escambia Co.: *Brinker 473* (MO). Hillsborough Co.: *Ferguson s. n.* (MO). Jefferson Co.: *Hitchcock s. n.* (MO). Lake Co.: *Nash 1309* (MO). Marion Co.: *Woodson & Schery 97* (MO). Volusia Co.: *Hood s. n.* (MO).

Georgia: Bulloch Co.: *Harper 946* (MO). Cobb Co.: *Duncan 8646* (MO). DeKalb Co.: *Miller, Perry, Boyd & Myers 531* (MO). Gwinnett Co.: *Allard 129* (MO). Madison Co.: *Duncan 11588* (MO). Oconee Co.: *Small s. n.* (MO). Stephens Co.: *Duncan 11737* (MO). Union Co.: *Duncan 7835* (MO). Whitfield Co.: *Harper 393* (MO).

Illinois: Jackson Co.: *Mohlenbrock 5058* (MO).

Kansas: Cowley Co.: *White 134* (MO). Montgomery Co.: *Rydberg & Imler 454* (MO).

Kentucky: McCreary Co.: *Wherry & Pennell 13873* (MO). Whitley Co.: *Wherry & Pennell 13843* (MO).

Louisiana: Rapides Parish: *Ball 621* (MO).

Maryland: Montgomery Co.: *Painter 1084* (MO).

Missouri: Barry Co.: *Bush 3265* (MO). Benton Co.: *Steyermark 24436* (MO), *24436a* (MO). Butler Co.: *Steyermark 11489* (MO). Callaway Co.: *Steyermark 26175* (MO). Camden Co.: *Steyermark 20655* (MO). Cole Co.: *Steyermark 14981* (MO). Crawford Co.: *Steyermark 15373* (MO). Dade Co.: *Steyermark 5653* (MO). Dent Co.: *Kellogg 995* (MO). Douglas Co.: *Steyermark 15373* (MO). Dunklin Co.: *Bush 6271* (MO). Franklin Co.: *Craig s. n.* (MO). Greene Co.: *Dewart 72* (MO). Henry Co.: *Steyermark 15948* (MO). Hickory Co.: *Steyermark 24488* (MO). Howell Co.: *Blankinship s. n.* (MO). Iron Co.: *Pammel s. n.* (MO). Jasper Co.: *Palmer 461* (MO). Jefferson Co.: *Steyermark 1366* (MO). Lincoln Co.: *Steyermark 8130* (MO). McDonald Co.: *Palmer 6a* (MO). Maries Co.: *Steyermark 15303* (MO). Marion Co.: *Davis 7866* (MO). Oregon Co.: *Palmer & Steyermark 41740* (MO). Pike Co.: *Steyermark 25893* (MO). Polk Co.: *Steyermark 23987* (MO). Ralls Co.: *Steyermark 25865* (MO). Reynolds Co.: *Steyermark 14201* (MO). Ripley Co.: *Mackenzie 327* (MO). St. Louis Co.: *Drushel 4311* (MO). Shannon Co.: *Bush s. n.* (MO). Stoddard Co.: *Steyermark 20763* (MO). Stone Co.: *Steyermark 22699* (MO). Taney Co.: *Palmer 5888* (MO). Vernon Co.: *Drouet 130* (MO). Wayne Co.: *Steyermark 11217* (MO). Webster Co.: *Steyermark 23897* (MO). Wright Co.: *Bush s. n.* (MO).

New Jersey: Burlington Co.: *Meredith s. n.* (MO). Camden Co.: *Martindale s. n.* (MO). Gloucester Co.: *Parker 12430* (MO). Hunterdon Co.: *Fisher s. n.* (MO). Middlesex Co.: *Mackenzie 2871* (MO). Ocean Co.: *Churchill s. n.* (MO). Salem Co.: *Meredith s. n.* (MO).

North Carolina: Cherokee Co.: *Fox 4034* (MO). Cumberland Co.: *Fox & Godfrey 2600* (MO). Edgecombe Co.: *Fox 4080* (MO). Harnett Co.: *Fox & Godfrey 2559* (MO). Henderson Co.: *Davis 9030* (MO). Hoke Co.: *Schallert s. n.* (MO). Orange Co.: *Wilson 28* (MO). Rowan Co.: *Heller 14005* (MO). Swain Co.: *Beardslee & Kofoid s. n.* (MO). Wayne Co.: *Fox, Godfrey & Boyce 4325* (MO).

Oklahoma: Caddo Co.: *Goodman 2342* (MO). Choctaw Co.: *Houghton 4025* (MO). Comanche Co.: *Stevens 1411* (MO). Johnston Co.: *Palmer 6438* (MO), *6438a* (MO). McCurtain Co.: *Houghton 3788* (MO). Payne Co.: *Stratton 188* (MO). Woods Co.: *White 277* (MO).

Pennsylvania: Bedford Co.: *Berkheimer 3458* (MO). Lancaster Co.: *Eisenhower s. n.* (MO). Montgomery Co.: *Redfield 1524* (MO). Philadelphia Co.: *Eby s. n.* (MO). Schuylkill Co.: *Collector Unknown* (MO). York Co.: *Glatfelter s. n.* (MO).

South Carolina: Aiken Co.: *Eggert s. n.* (MO). Anderson Co.: *Davis 8441* (MO). Dillon Co.: *Godfrey SC49040* (MO). Georgetown Co.: *Godfrey 146* (MO). Laurens Co.: *Davis s. n.* (MO). Oconee Co.: *Duncan 11255* (MO). Pickens Co.: *Rodgers 385* (MO).

Tennessee: Cocke Co.: *Kearney 675* (MO); *Kearney 674* (MO).

Texas: Bowie Co.: *Eggert s. n.* (MO). Brazos Co.: *Palmer 11750* (MO). Dallas Co.: *Reverchon 193* (MO). Harris Co.: *Boon 185* (MO). Lee Co.: *Eggert s. n.* (MO). Nacogdoches Co.: *Parks RX2287* (MO). Parker Co.: *Tracy 8025* (MO). Travis Co.: *Buckley s. n.* (MO). Waller Co.: *Hall 153* (MO).

Virginia: Smyth Co.: *Small s. n.* (MO).

West Virginia: Jackson Co.: *Berkley 816* (MO). Lincoln Co.: *Berkley 899* (MO). Summers Co.: *Fox 2481* (MO).

16. Stylosanthes guyanensis (Aubl.) Sw. Svenska Vet. Akad. Handl. 11:296. 1789.

Stems herbaceous or mostly suffruticose, erect or rarely scandent, to 1 m. tall, glabrous to puberulent to pilose or often hispid or setose, the setae often purplish. Leaflets green to purple, lanceolate to elliptic to nearly ovate, acute or occasionally obtuse at the apex, glabrous to puberulent to tuberculate-bristly, particularly on the margins and the costa beneath, sometimes spinulose-toothed, with 2–7 pairs of nerves, the terminal usually 5–30 mm. long and 2–10 mm. broad (rarely to 45 mm. long and 20 mm. broad), the lateral ones slightly smaller than the terminal; petioles 1–10 mm. long, sometimes canaliculate above, glabrous to puberulent to setose, the rhachis 0.5–1.5 mm. long; sheath of the stipules glabrous to pilose to setose, 2–15 mm. long, 3- to many-nerved, the subulate teeth 2–10 mm. long. Spikes small, narrow, and 2-flowered to large, globose, and about 40-flowered; bracts mostly unifoliolate, the leaflet sometimes much reduced and often spinulose-toothed, the sheaths green to purple, glabrous to puberulent to bristly, 3–7 mm. long, 3- to 9-nerved; outer bracteole 1, lanceolate or ovate, 2.5–3.0 mm. long, acuminate, glabrous to pilose, occasionally purplish at the apex; axis rudiment none; inner bracteole 1, 2–3 mm. long, acuminate, glabrous to pilose, colored like the outer bracteole. Calyx tube 4–8 mm. long, glabrous to sparsely pubescent, the

lobes 3–5 mm. long, obtuse to acute, ciliate or sometimes pilose. Standard 4–8 mm. long, 3–5 mm. broad, suborbiculate; wings 3.5–5.0 mm. long, auriculate, spurred within at the base; keel petals 3.5–5.0 mm. long, falcate. Loment 1.5–2.5 mm. broad, reticulate; only the upper articulation fertile, glabrous to minutely short-pubescent near the apex, or occasionally with sessile glands near the apex, ovoid, plump, 2–3 mm. long; beak minute, 0.1–0.5 mm. long, strongly inflexed.

KEY TO THE SUBSPECIES

a. Leaflets green, usually 10–60 mm. long, sometimes tuberculate-bristly but not spinulose-toothed; internodes usually much greater than 1.5 cm. long; inflorescence mostly 5- to 40-flowered. Central America, South America............................16a. *S. guyanensis* ssp. *guyanensis*

aa. Leaflets purplish, 4–12 mm. long, densely and shortly tuberculate-bristly on the margin and the costa, appearing short-serrate; internodes 0.5–1.5 cm. long; inflorescence 1- to 4-flowered. Mexico..16b. *S. guyanensis* ssp. *dissitiflora*

Stylosanthes guyanensis is a most variable species. The leaflets range from small and lanceolate to large and elliptic. The indument of the stem is diverse. The spikes are large and to 40-flowered to small and 1- to 2-flowered. Numerous subspecies, varieties, and forms have been proposed, but intergradations occur between almost all. Except for subspecies *dissitiflora*, there is no strong geographical correlation with any of the variants. A great number of the most southern specimens are 40-flowered and bristly and the northern specimens 5- to 20-flowered and more or less viscid, but this is far from constant.

Great confusion as to the proper name for this species has arisen. Aublet described *Trifolium guyanense* as having pubescent loments and illustrated it thus. The type photograph, however, appears to coincide with many of the specimens examined in this study with glabrous or puberulent loments. Those considering Aublet's *T. guyanense* as inapplicable to present known specimens employ the binomial *S. gracilis* for this broad species.

Numerous other morphological extremes have been proposed: *S. hispida* Rich. with densely hispid stems; *S. surinamensis* Miq. with rather narrow leaflets; *S. ruellioides* Benth. with densely pubescent stems and broad leaflets; *S. longiseta* Micheli with the stems bearing long bristles; and *S. pohliana* Taub. with acuminate leaflets. *Stylosanthes ingrata* Blake from Vaca Falls, British Honduras, is without fruit but seems to be *S. guyanensis* ssp. *guyanensis*.

Stylosanthes guyanensis ssp. *guyanensis* occurs from Central America through South America into northern Argentina, also in the Antilles. It has been planted in Australia in an effort to impede soil erosion. *Stylosanthes guyanensis* ssp. *dissitiflora* is limited to a small area in southwestern Mexico. It occurs at altitudes between 3500 and 5000 feet.

16a. Stylosanthes guyanensis ssp. guyanensis

Trifolium guyanense Aubl. Pl. Guian. 776. 1775, ex char. (T: *Aublet s. n.*, photo!)
Stylosanthes hispida Rich. Act. Soc. Hist. Nat. Par. 2:112. 1792, ex char.
Stylosanthes gracilis HBK. Nov. Gen. et Sp. 6:507. 1823, ex char.
Stylosanthes surinamensis Miq. in Linnaea 18:567. 1844, ex char.
Stylosanthes ruellioides Benth. in Mart. Fl. Bras. 15^1:90. 1859, ex char.
Stylosanthes guyanensis β subviscosa Benth. loc. cit. 92. 1859, ex char.
Stylosanthes longiseta Micheli, in Mem. Soc. Phys. Genève 28:7. 1883, ex char.
Stylosanthes pohliana Taub. in Verh. Bot. Brand. 32:29. 1890. (T: *Pohl 1997*!)
Stylosanthes guyanensis var. *pubescens* Pilger, in Engl. Bot. Jahrb. 30:160. 1901, ex char. (T: *Pilger 286*).
Stylosanthes juncea f. *intermedia* Chod. & Hass. in Bull. Herb. Boiss. ser. 2, 4:884. 1904. (T: *Hassler 3781*).
Stylosanthes montevidensis var. *longiseta* (Micheli) Chod. & Hass. loc. cit. 885. 1904. (T: *Hassler 4573*).
Stylosanthes guyanensis var. *genuina* Hass. in Fedde, Rep. Sp. Nov. 16:220. 1919. (T: *Hassler 7781*!)
Stylosanthes guyanensis var. *genuina* f. *esetosa* Hass. in Fedde, loc. cit. 221. 1919. (T: *Hassler 2834*!)
Stylosanthes guyanensis var. *intermedia* (Vog.) Hass. in Fedde, loc. cit. 1919.
Stylosanthes guyanensis var. *intermedia* ssp. *anomala* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes guyanensis var. *subviscosa* f. *viscosissima* Hass. in Fedde, loc. cit. 1919. (T: *Hassler 6454*!)
Stylosanthes guyanensis var. *longiseta* (Micheli) Hass. in Fedde, loc. cit. 222. 1919.
Stylosanthes guyanensis var. *marginata* Hass. in Fedde, loc. cit. 223. 1919. (T: *Hassler 9938*!)
Stylosanthes ingrata Blake, in Proc. Biol. Soc. Wash. 39:51. 1928. (T: *Record s. n.*!)
Stylosanthes gracilis var. *vulgaris* Burkart, in Darwiniana 3:247. 1939, ex char.
Stylosanthes gracilis var. *subviscosa* (Benth.) Burkart, loc. cit. 248. 1939.

British West Indies: trinidad: St. Joseph savanna, *Britton, Hazen & Broadway 976* (GH, US, NY).

British Honduras: belize: Belize, *Bartlett 11250* (US, NY). cayo: Mt. Pine Ridge, *Bartlett 11706* (US, GH); Vaca Falls, *Record s. n.* (US). stann creek: Stann Creek, *Schipp 486* (MO, GH, NY, F); Stann Creek, *Gentle 1883* (MO, GH, NY, F). toledo: Swasey Branch, Monkey River, *Gentle 3898* (GH, F, US, NY, MO).

Costa Rica: cartago: Juan Viñas, *Rowlee & Stork 839* (NY, US). Cartago, *Léon 186* (F). heredia: Santa Barbara, *Pittier 1656* (US). san josé: Santiago, *Brenes 14326* (GH, US); San José, *Tonduz 2169* (US, GH); El General, *Skutch 2462* (NY, US); San Pedro de la Calabaza, *Tonduz 10919* (US); Santa María, *Standley 41595* (US); between Aserrí and Tarbaca, *Standley 34031* (US). without precise locality: Boruca, *Tonduz 4707* (US); Río Colorado, *Valerio 278* (F).

El Salvador: la libertad: between Finca Germania and Finca San Antonio, near Comasagua, *Carlson 250* (F). san salvador: from San Martín to Laguna de Ilopango, *Standley 22523* (US, NY); exact locality unknown, *Calderón 1133* (US, NY), *1287* (GH, US, NY); *Standley 19398* (NY, GH, US), *Velasco 8963, 8995* (US). santa ana: vicinity of Metapan, *Standley & Padilla 3098* (F), *3261* (F). san vicente: San Vicente, *Standley 21318* (US, GH, NY).

Guatemala: alta verapaz: Coban, *Standley 70111* (NY, F); Coban, *von Türckheim 84* (US). chimaltenango: Alameda, *Johnston 346* (F); from Chimaltenango to San Martín Jilotepeque, *Standley 57982* (GH, NY, F); San Martín Jilotepeque, *Standley 64402* (NY, F); San Juan-Malagua, *Johnston 1555* (F). chiquimula: El Rincón, *Standley 74734* (F). escuintla: along Río Guacalate, *Standley 89369* (F), *58200* (F); Finca El Zapote, *Muenscher 12417* (F); near Escuintla, *Standley 63577* (GH, F). guatemala: Finca Bretaña, between Guatemala and Fiscal, *Standley 59690* (F); near Finca La Aurora, *Aguilar 18* (F); Chilloní, *Rojas 47* (US); exact locality unknown, *Salas 529*

(US). HUEHUETENANGO: along Río Cuilco, between Cuilco and San Juan, *Steyermark 50838* (F); Río Pucal, *Standley 65833* (F); east of San Rafael Pétzal, *Standley 83051* (F), *83076* (F); 14 miles south of Huehuetenango, *Standley 82398* (F). IZABAL: between Los Amates and Izabal, *Kellermann 7556* (NY, F), *7257* (NY, F); between Milla and Cristina, *Steyermark 38355* (F), *38653* (F); Gualán, *Blake 7691* (US); Cristina, *Blake 7585* (US); Quiriguá, *Standley 24223* (GH, US); near Quiriguá, *Standley 72470* (F). JALAPA: vicinity of Jalapa, *Standley 76661* (F); northeast of Jalapa, *Standley 76803* (F). JUTIAPA: vicinity of Jutiapa, *Standley 75042, 75511* (F). QUEZALTENANGO: Colomba, *Skutch 2048* (US, GH, F). QUICHÉ: between Cotzal and San Francisco, *Sharp 45169* (F); exact locality unknown, *Aguilar 1490* (F). RETALHULEU: near Retalhuleu, *Standley 88622* (F). SACATEPÉQUEZ: Barranco Hondo, *Standley 60232* (GH, F); Santa María de Jesús, *Standley 59401* (GH, NY, F); Ciudad Vieja, *Tejada 273* (US); near Antigua, *Standley 61723* (F). SANTA ROSA: southeast of Barberena, *Standley 77879* (F); Buena Vista, *Heyde & Lux 3752* (F); La Vega, *Heyde & Lux 4457* (US, GH). SUCHITEPÉQUEZ: Finca Las Nubes, *Steyermark 35442* (F); Tinca Mocá, *Skutch 1463* (GH). ZACAPA: Sierra de las Minas, *Steyermark 29647* (F).

HONDURAS: CHOLUTECA: vicinity of San Marcos de Colón, *Standley 15706* (US). COMAYAGUA: Siguatepeque, *Standley 56264* (US, F); vicinity of Comayagua, *Standley & Chacón 5972* (F); El Achote, near Siguatepeque, *Standley 56148* (F). COPÁN: Hacienda Espiritu Sancto, *Blake s. n.* (US). MORAZÁN: El Zamorano, *Molina 61* (F, US); San Antonio del Oriente, *Rodríguez 668* (F), *687* (F); Piedra Parada, *Standley 11937* (F); near Joya Grande, *Standley & Molina 4466* (F); Guaimaca, *Molina 2906* (F). OLANCHO: from Catacamas to Loma Pelona, *Standley 18283* (F). EL PARAÍSO: Quebrada de Dantas, *Standley, Williams & Molina 1260* (F); Yuscarán, *Molina 1694* (F); west of Güinope, *Merrill & Williams 15713* (F); Manzaragua Road, *Williams & Molina 11484* (MO, GH, F); Ofo de Agua, *Williams & Molina 12027* (GH, F); Güinope, *Rodríguez 1678* (F). SANTA BÁRBARA: Los Dragos, *Standley & Lindelie 7405* (F).

MEXICO: CHIAPAS: exact locality unknown, *Doyle 144* (US). JALAPA: Hacienda de la Laguna, *Schiede 631* (NY). JALISCO: San Sebastian, *Nelson 4075* (US, GH). OAXACA: Jalapa, *Pringle 9174* (GH). PUEBLA: Metlatoyuca, *Goldman 57* (GH, US). VERACRUZ: Minatitlan, *Mell s. n.* (NY); Zacuapan, *Purpus 1888* (NY, MO, US, GH, F); Orizaba, *Botteri 152* (GH). WITHOUT PRECISE LOCALITY: Lodiego, *Palmer 1900* (NY, GH, US, F); Monte Cristo, *Matuda 1958* (US, NY, GH); Vallecitos, Montes de Oca, *Hinton 11456* (US).

NICARAGUA: GRANADA: near Granada, *Grant 756* (GH). JINOTEGA: San Rafael del Norte, *Miller & Griscom 66* (US); southwest of Jinotega, *Standley 9534* (F), *10082* (F), *10094* (F).

PANAMA: CANAL ZONE: Sosa Hill, Balboa, *Standley 26443* (US); between Fort Clayton and Corozal, *Standley 29159* (US); Summit, *Standley 30068* (US); along Las Cruces Trail, *Hunter & Allen 753* (GH, MO); Río Puente, *Dodge, Steyermark & Allen 16835* (GH); Empire to Mandinga, *Piper 5129* (US). CHIRIQUÍ: Volcancitos, *Terry 1264* (GH, US, MO, F); COCLÉ: Penonomé, *Williams 167* (US, NY), *148* (US, NY); Natá, *Allen 838* (GH, US, MO, NY). PANAMÁ: Sabanaz, *Standley 25837* (US); Taboga Island, *Standley 28013* (US); between Matías Hernández and Juan Díaz, *Standley 32077* (US); Chêpo, *Hunter & Allen 75* (MO, GH); Pacora, *Bro. Maurice 790* (US).

ARGENTINA: CÓRDOBA: Sierra Chicas, Estancia la Reduccíon, *Burkart 7397* (F). CORRIENTES: Estancia, Santa Teresa, *Pedersen 79* (US). MISSIONES: Santa Ana, *Rodríguez 756* (MO); Posadas, *Ekman 1742* (NY); San Ignacio, *Ekman 1740* (US).

BOLIVIA: LA PAZ: Guanai-Tipuani, *Bang 1459* (MO, US, GH, NY, F); Nord Yungas, Coripata, *Büchtien 8101* (US, NY); Tipuani, *Büchtien 5423* (US, GH, MO, NY, F); South Yungas, San Bartolomé, near Calisaya, *Krukoff 10536* (US, MO, NY, F); Tampa, *Büchtien 1787* (US); La Joya, *Tate 1031* (NY); Mapiri, *Tate 466* (NY), *471* (NY); near La Paz, *Rusby 1008* (NY); Guanai, *Rusby 2324* (NY). SANTA CRUZ: Velasco, *Kuntze s. n.* (NY, US, F); Sará, Buena Vista, *Steinbach 6916* (GH, NY, F, MO); San José, *Williams 384* (US). WITHOUT PRECISE LOCALITY: Eskia, *White 612* (NY).

BRAZIL: BAÍA: Mucugé, Serra Sincorá, *Froes 20128* (NY). CEARÁ: Lagoa Porangaba, Fortaleza, *Drouet 2726* (GH, US, F). DISTRITO FEDERAL: Praía de Sernambetiba, *L. B. Smith 6359* (US). GOIÁS: Corgo do Jaraguá, *Pohl 949* (NY); Quexada, *Maceil 2132* (MO). MINAS GERAES: São Sebastião do Paraíso, *Vidal 3659* (GH); Caldas, *Regnell III428* (US); Uberaba, *Regnell 430* (US); Ilheos, *Moricand s. n.* (GH); Viçosa, *Mexía 4523* (NY, GH, US, MO, F); near Lagôa Pampulha, *Williams & Assis 6084* (GH); Estacão de Barreiro, *Williams & Assis 7122* (GH); Belo Horizonte, *Williams & Assis 5832* (GH, US); Bento Pires, *Williams & Moreira 5219* (GH); Tijuco, *Riedel 1316* (US); Canga, *Magalhaes 1760* (US); Engenho Nogueira, *Magalhaes 3168* (US); Santa Luzia, Chapeu de Sol, *Archer & Barreto 5015* (US); Jaboticatubas, *L. B. Smith 7078* (US); Diamantina, *Archer 4084* (US); Serra do Taquaril, *Barreto 5771* (F); Ituiutaba, *Macedo 1670* (US). PARÁ: Vigia, Campina do Palha, *Pires 4083* (NY); Gurupá, *Ducke 16182* (US); Colares, *Poeppig 2930* (NY); Belém, *Baldwin 4557* (US). PARAÍBA: Areia, *de Moraes 885* (NY). PARANÁ: Villa Velha, *Dusén 14781* (GH, F); Morungaba, *Dusén 16568* (GH); Tibagy, *Reiss 75a* (NY, F); Jaguariaiva, *Dusén 16381* (GH), *16596* (MO). PERNAMBUCO: Tapera, *Pickel 2403* (US). RIO DE JANEIRO: Cabo Frio, *Rose & Russell 20693* (US); Tijuca, *Riedel 1256* (US). SÃO PÁULO: Butantan, *Hoehne 137* (NY, GH); Iparanga, *Luederwaldt 13323* (NY); Capivari, *Riedel 1316* (US). WITHOUT PRECISE LOCALITY: Serra do Cipo, Conceicao, *Barreto 8994* (F); Rio Claro and Poracutu, *Pohl 2107* (NY); Socaja, *Mikan s. n.* (NY); Corrego Padre, *Pohl 1997* (NY, F).

BRITISH GUIANA: Pirara, *Schomburgk 381* (US); basin of Rupununi River, near mouth of Charwair Creek, *A. C. Smith 2376* (MO, NY, US, F); Orealla savanna, Berbice, *Irwin 330* (US); exact locality unknown, *Schomburgk 240* (US).

COLOMBIA: ANTIOQUÍA: Hayo Rico, *Corres & Barkley 18A200* (US); Medellín, *Archer 644* (US); Bello, *Archer 436* (US); San Antonio, *Bro. Daniel 530* (US, F); Fredonia, *Bro. Tomas 957* (US); El Prado, *Bro. Tomas 1009* (US); El Carmen, *Bro. Daniel 2310* (US). BOGOTÁ: Caqueza, *Traina 4327* (US). BOYACÁ: Mt. Chepon, *Lawrence 332* (NY, GH, F). CAUCA: Popayán, *Lehmann 2855* (US); El Tambo, *von Sneidern 1414* (NY, US); Albán, San José, *Arbeláez 2382* (US); Valle del Cauca, *Traina 4323* (NY); La Paila, *Holton 955* (NY); Cuatro Esquinas, *Pennell & Killip 6352* (US, NY). CUNDINAMARCA: La Esperanza, *Cuatrecasas 2472* (US); San Francisco, *Garcia-Barriga 10981* (US); Estación Santana, *Dugand & Jaramillo 3831* (US, NY); Sasaima, *Bro. Ricardo s. n.* (US); Quetame, *André 1113* (F); Soncha, *André 1474* (F). HUILA: east of Neiva, *Rusby & Pennell 1111* (NY); San Augustín, *Bro. Daniel 4127* (US, F). MAGDALENA: Pueblo Bello, Valle Dupar, *Bro. Angel 673* (US); Santa Marta, Jordan, *H. H. Smith 58* (US, NY, GH, F); Jagua, *Allen 688* (MO). META: Cabuyaro, *Sprague s. n.* (US); Las Lagartija, southwest of Uribe, *Fosberg 19414* (US); Villavicencio, *Bro. Apollinaire s. n.* (US); El Mico airstrip, *Philipson, Idrobo & Fernandez 1310* (US). NORTE DE SANTANDER: del Sarare, Río Cubucón, *Cuatrecasas 18608* (US, F). SANTANDER: Río Casanare, Esmeralda, Los Llanos, *Cuatrecasas 3824a* (F). TOLIMA: Libano, *Pennell 3351* (NY); west of San Lorenzo, *Pennell 3491* (NY, US, GH); Mariquita, *Pennell 3673* (US, NY, GH). EL VALLE: Samaria, on Río Timba, near Timba, *Fosberg 20518* (NY, US); Las Neives, west of Cali, *Killip, Cuatrecasas & Dryander 39200* (US, F); Pavas, *Pennell 5505* (NY, GH), *5532* (GH, US); Dagua, *Arbeláez 3015* (US); east of Zarzal, *Pennell, Killip & Hazen 8461* (GH, NY, US); Santa Rosa, *Pennell & Killip 6073* (US, NY); Río Cali, Pichindé, *Duque 1650* (US); Cerro de Tres Cumbres, *Bermúdez & Barkley 17C845* (US); Cartago, Cuchilla de Santa Bárbara, *Cuatrecasas 22966* (US); El Forge, near Buenaventura, *Killip & Cuatrecasas 38938* (US, F). VAUPÉS: Río Guaviare, San José del Guaviare, *Cuatrecasas 7653a* (US). WITHOUT PRECISE LOCALITY: no location given, *Mutis 2345* (US), *2976* (US), *4683* (US).

ECUADOR: exact locality unknown, *Espinosa 590* (US).

FRENCH GUIANA: vicinity of Cayenne, *Broadway 709* (NY); west of Cayenne, *Cowan & Maguire 38013* (NY); exact locality unknown, *Bentham 20* (NY).

PARAGUAY: AMAMBAY: Sierra de Amambay, *Hassler 12043* (NY, F). CAAGUAZA: Yhú, *Hassler 9532* (NY, GH). CENTRAL: Cerros de Tobatí, *Hassler 6454* (GH, NY). LA CORDILLERA: Cordillera de Altos, *Fiebrig 405* (GH). SAN PEDRO: San Estanislão,

Hassler 6014 (GH, NY), *5996* (NY, GH), *7030* (NY, GH), *7081* (NY). WITHOUT PRECISE LOCALITY: Centurion, *Fiebrig 4397* (GH, US); Santa Elísa, *Hassler 2834* (MO, GH); Berghang, San Luis, *Fiebrig 4453-4413* (GH).

PERU: AYACUCHO: Aino, *Killip & Smith 22605* (NY, US). CUZCO: San Pedro, *Vargas 2576* (GH); Valle de Santa Ana, *Herrera 3614* (F). JUNÍN: Chanchosmayo Valley, *Schunke 1410, 1412, 1518* (F). SAN MARTÍN: near Moyobamba, *Klug 3638* (NY, GH, US, MO, F); Tarapoto, *Woytkowski 35097* (MO, F). TUMBES: La Palma, *Anderson 948* (US).

SURINAM: Republiek, *Kuyper 18* (US); Coppename River, Volksberg, *Pulle 279* (MO).

VENEZUELA: ANZOÁTEQUI: Los Caños, *Pittier 14472* (US); Río Cani, *Garroni 62* (US). BOLÍVAR: Gran Sabana, Hato Santo Teresa, *Tomayo 3202* (US); between Ciudad Bolívar and El Cristo, *Killip 37217* (US); Caño Piña, *Cardona 614* (US). COPEDES: San Carlos, *Rudd 331* (US). DISTRITO FEDERAL: Turmerito, *Killip 37138* (US, NY); Caracas, *Bailey & Bailey 97* (US); El Limón, *Williams 10540* (F). MÉRIDA: Tovar, *Fendler 297* (GH, MO); Montes de Zerpa, *Lossen 314* (US). MONAGAS: between Caripe and San Augustín, *Steyermark, 61783* (MO, F). TRUJILLO: Carretera Trujillo-Boconó, *Tomayo 1846* (US); Escuque, *Pittier 13150* (NY, MO, US). ZULIA: Mene Grande, *Pittier 10588* (US). WITHOUT PRECISE LOCALITY: Tobay, *Gehriger 358* (MO); Entrada, *Warming 100* (US).

Fig. 6

16b. Stylosanthes guyanensis ssp. **dissitiflora** (Robins. & Seat.) Mohlenbrock, stat. nov.

Stylosanthes dissitiflora Robins. & Seat. in Proc. Am. Acad. 28:105. 1893. (T: [Pringle] ~~*Robinson & Seaton*~~ *5172*!)
Stylosanthes purpurata Blake, in Proc. Biol. Soc. Wash. 33:52. 1920. (T: *Rose 2942*!)
Stylosanthes eciliata Blake, in Univ. Calif. Publ. Bot. 10:409. 1924. (T: *Purpus 9246*!)

Mexico: jalisco: near Guadalajara, *Rose & Painter 7478* (US, GH); southwest of Autlán, *McVaugh 14222* (US); near Etzatlán, *Rose & Painter 7543* (US, NY); Río Blanco near Guadalajara, *Pringle 11433* (US, GH); near Guadalajara, *Pringle 5172* (GH).

17. Stylosanthes angustifolia Vog. in Linnaea 12:63. 1838, ex char. (T: *Sellow s. n.*)

Stylosanthes angustissima Klotzsch, in Schomburgk, Faun. Fl. Brit. Guin. 1200. 1840, ex char.
Astyposanthes angustifolia (Vog.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems usually woody below, erect, much branched from the base, to 1 m. tall, slender, densely long-hispid or glabrescent. Leaflets linear to linear-lanceolate, acuminate, to 40 mm. long and 2.5 mm. broad, glabrous or rarely with scattered bristles on both surfaces, the margins often involute; petioles 2–16 mm. long, shortly bristly or nearly glabrous, the rhachis 1.5–3.5 mm. long; sheath of the stipules 3.5–7.0 mm. long, glabrous or usually with long tuberculate bristles and often villous, 5- to 9-nerved, the subulate teeth 2.5–4.5 mm. long. Spikes elongate, narrow, to 45 mm. long, 3- to 20-flowered; bracts unifoliolate, the leaflet often reduced to a small laminal projection, the sheath villous and usually with long bristles, 3–4 mm. long, 9- to 11-nerved, the teeth 2.0–3.5 mm. long; outer bracteole 1, 2.5–3.0 mm. long, ciliate near the apex; axis rudiment none; inner bracteole 1, 2.5–3.0 mm. long, ciliate. Calyx tube 3.5–5.0 mm. long, the lobes 1.5–2.5 mm. long and usually ciliate. Standard suborbiculate, 3.5–4.0 mm. long; wings 3–4 mm. long, auriculate at the base, shortly appendaged within; keel petals falcate, 1.5–2.5 mm. long, densely white hairy. Loment 0.8–1.5 mm. broad, 2–3 mm. long, faintly nerved, minutely pubescent, with only the small upper articulation fertile; beak 2.5–4.0 mm. long, strongly uncinate to circinate, usually over twice as long as the upper articulation.

Stylosanthes angustifolia seems to prefer low sandy areas in woods. It is known from British Guiana, French Guiana, Surinam, and northern Brazil (fig. 7).

Brazil: ceará: margins of Açude Boa Agua, *Drouet 2422* (GH, F); Bairro do Tanape, Fortaleza, *Drouet 2366* (GH, NY, US, F). maranhão: exact locality unknown, *Gardner 6000* (GH). pará: Ilha do Mosqueiro, *Killip & Smith 30423* (NY, US); near Santarem, *Spruce s. n.* (GH, NY); exact locality unknown, *Tavares 13* (NY). piauí: exact locality unknown, *Gardner 2094* (NY). rio branco: Caracarahy, *Froes 23664* (NY); Surumu, *Ule 8161* (US). rio grande do norte: Angicos, *Swallen 4715* (US). without precise locality: tropics, *Burchell 9004* (GH, NY).

British Guiana: Roraima, *R. Schomburgk 536* (NY).

French Guiana: Cayenne, *Rothery s. n.* (NY).

Surinam: Wayombo River, *Linder 97* (GH, NY); Joden, *Kegel 1113A* (NY); Saron, *Kegel 1113B* (NY); Sectie Oeest, *Pulle 139* (US, MO); near Zanderij Island, *Archer 2813* (US); exact locality unknown, *Hostmann 1018* (NY, MO).

18. STYLOSANTHES LEIOCARPA Vog. in Linnaea 12:64. 1838. (T: *Sellow 4235*!)

Astyposanthes leiocarpa (Vog.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems herbaceous to somewhat woody at the base, simple to much branched, ascending to suberect, nearly 0.5 m. tall, often viscid, densely and shortly bristly to glabrous near the base. Leaflets usually oblong, mucronulate at the apex, the terminal to 15 mm. long and 3 mm. broad, the lateral to 12 mm. long and 3 mm. broad, with short tuberculate-based bristles on both surfaces, with 2–4 pairs of very obscure veins not forming any submarginal nerve; petioles 3.5–4.5 mm. long, hispidulous, the rhachis 1.5–2.0 mm. long; stipular sheaths 4–6 mm. long, with 9–11 distinct veins, long-bristly, the subulate teeth 5–6 mm. long. Spikes 2.5–4.0 mm. long, 8- to 10-flowered; bracts unifoliolate, the leaflet hispid to short-bristly, the sheaths bristly, 3.5–4.5 mm. long with 7, rarely 9–11 veins, the teeth 2.5–3.5 mm. long; outer bracteole 1, 2.5–3.0 mm. long, ciliate near the tip; axis rudiment none; inner bracteole 1, 2.0–2.5 mm. long and ciliate. Calyx tube 2.5–3.0 mm. long, the lobes 2.0–2.5 mm. long and ciliate. Standard suborbiculate, 4–6 mm. long; wings 3.5–5.0 mm. long, auriculate, spurred within at the base; keel petals 3.5–4.5 mm. long, falcate. Loment reticulate with 1 or 2 additional longitudinal nerves besides the reticulate venation, about 2 mm. broad; both articulations fertile, or the upper sometimes abortive, or the lower abortive; upper articulation when fertile 2–3 mm. long and glabrous, the lower, when fertile, 1.5–3.5 mm. long and glabrous; beak somewhat uncinate or nearly straight, 2.0–2.5 mm. long, glabrous.

The species is known only through a few collections from Uruguay, Paraguay, southern Brazil, and southern Colombia. A specimen collected by Arsène from Morelia, Mexico, is obviously *S. leiocarpa*, but this extreme extension of the range seems unlikely. A note penciled on the sheet by S. F. Blake in 1924 states that this is "probably one of the sheets distributed by Otto Weigel and is badly mixed."

BRAZIL: MINAS GERAES: Osorio, Morro Grande, *Rambo S1747* (US). RIO GRANDE DO SUL: São Leopoldo, *Leite 1909* (GH); São João do Monte Negro, *Bornmüller 657* (GH). SANTA CATARINA: Palhoca Massiambú, *Reitz & Klein 653* (US).

PARAGUAY: exact locality unknown, *Hassler 7575* (NY).

URUGUAY: MONTEVIDEO: Pooitos/Carrasco, *Herter 76691* (GH, NY, MO, F); Montevideo, *Baratini s. n.* (MO); Carrasco, *Osten 6498* (US). SAN JOSÉ: Barra, *Herter 89069* (MO). WITHOUT PRECISE LOCALITY: Cabo Santa Maria, *Rosengurtt B2471* (NY).

19. STYLOSANTHES **cayennensis** Mohlenbrock, sp. nov.

Herba erecta ad 30 cm. alta caulibus parce ramosis glabris vel puberulis. Foliola elliptico-lanceolata supra glabra subtus punctulata puberula setosa nervis 4–6-gemmatis; foliolo terminali ad 12 mm. longo 3.5 mm. lato; petiolo 2–4 mm. longo glabro vel puberulo; rhachide 1–2 mm. longa; stipulae striatae vagina 3–6 mm. longa saepissime puberula processibus subulato-mucronatis setosis 3–5 mm. longis. Spicae densae oblongoideae floribus 3–10; bracteis plerumque unifoliolatis stipuliformibus vagina puberula vel setosa 3–6 mm. longa nervis 5; bracteola exteri-

Fig. 7

ore 1, 2.5–3.0 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.5–3.0 mm. longa apice ciliata. Calycis tubus 3.5–5.0 mm. longus glaber lobis 1.5–2.5 mm. longis. Corolla lutea; vexillo suborbiculato 4–5 mm. longo; alis falcatis 3.5–4.0 mm. longis; carina falcata 3.5–4.0 mm. longa. Lomentum 1.5–2.0 mm. latum reticulatum, articulo superiore 2 mm. longo glabro vel raro puberulo, articulo inferiore 1.5–2.0 mm. longo glabro, rostro circa 1 mm. longo valde uncinato vel circinato glabro.

Known only from wet habitats in the vicinity of Cayenne, French Guiana. It is related to S. *guyanensis* because of the glabrous loments and the short strongly uncinate beak but differs in its bi-articulate loments.

French Guiana: vicinity of Cayenne, *Broadway 231* (US, NY, GH), *672* (NY, GH), *972* (GH, holotype).

20. STYLOSANTHES **hippocampoides** Mohlenbrock, sp. nov.

Herba erecta ad 60 cm. alta caulibus parce ramosis setosis. Foliola lineari-lanceolata supra setosula subtus setosa nervis 3–4-gemmatis; foliolo terminali ad 15 mm. longo 2.5 mm. lato; foliolis lateralibus ad 15 mm. longis 2 mm. latis; petiolo 2–4 mm. longo puberulo vel setosulo; rhachide circa 1 mm. longa; stipulae striatae vagina 3–8 mm. longa glabra vel setosula processibus subulatis mucronatis setosis 3–5 mm. longis. Spicae densae ovatae floribus 2–6; bracteis plerumque unifoliolatis stipuliformibus vagina setosa 3–6 mm. longa; bracteola exteriore 1, 2–3 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.0–2.5 mm. longa, apice ciliata. Calycis tubus 3.0–5.5 mm. longus glaber lobis 1.5–3.0 mm. longis. Corolla lutea; vexillo suborbiculato 3.5–5.5 mm. longo; alis falcatis 3–4 mm. longis; carina falcata 3.0–3.5 mm. longa. Lomentum circa 2 mm. latum valde reticulatum, articulo superiore 2.5–3.0 mm. longo glabro, articulo inferiore abortivo, rostro 2 mm. longo uncinato glabro.

Stylosanthes hippocampoides closely resembles *S. montevidensis* and *S. macrosoma*. *Stylosanthes hippocampoides* has conspicuously reticulate, glabrous loments about as broad as long and a 4- to 8-flowered inflorescence; *Stylosanthes macrosoma* has obscurely nerved, glabrous loments about twice as long as broad and a 2- to 6-flowered inflorescence; *Stylosanthes montevidensis* has a reticulate-nerved, pubescent loment about as broad as long and a 4- to 40- flowered inflorescence. The specific epithet is derived from the loment which superficially is shaped like the sea-horse (*Hippocampus*).

The species is infrequent in Uruguay and northern Argentina. Some specimens were included by Burkart in his *S. gracilis* var. *rostrata*. The presence of a distinct beak on the loment clearly distinguishes this species from *S. gracilis* of Burkart.

ARGENTINA: CÓRDOBA: Unquillo, *Cabrera s. n.* (F); Sierra Chica, *Kurtz s. n.* (NY); Sierra Achala, *Kurtz 8303* (NY, HOLOTYPE); Potrera de Loza, *Galander s. n.* (NY). CORRIENTES: Ituzaingo, Puerte Loreto, *Schuranz s. n.* (US); exact locality unknown, *Burkart 6743* (GH). MISIONES: Concepción, *Clos 2023* (GH).

URUGUAY: COLÓNIA: Riachuelo, *Herter 15562* (GH, US, NY, MO, F); exact locality unknown, *Clos 3231* (GH).

21. STYLOSANTHES MACROSOMA Blake, in Proc. Biol. Soc. Wash. 33:52. 1920. (T: *Morong 255*!)

Stylosanthes montevidensis f. *arenosa* Hass. in Fedde, Rep. Sp. Nov. 16:223. 1919, ex char.

Stems ligneous near the base, erect, branched, to 2 dm. tall, with soft white pubescence and some scattered tuberculate bristles. Leaflets narrowly elliptic, mucronate, acute, nearly glabrous above but with scattered bristles beneath, with 3–4 pairs of conspicuous veins forming a submarginal nerve; terminal leaflet to 14 mm. long and 2.5 mm. broad; petioles 3–5 mm. long, with scattered short bristles, the rhachis 1 mm. long or less; sheath of the stipules 4.5–5.5 mm. long, with scattered bristles, 11- to 15-nerved, the subulate teeth 3–4 mm. long. Spikes oblongoid to ovoid, 2- to 4-flowered; bracts unifoliolate, the leaflet 4–7 mm. long,

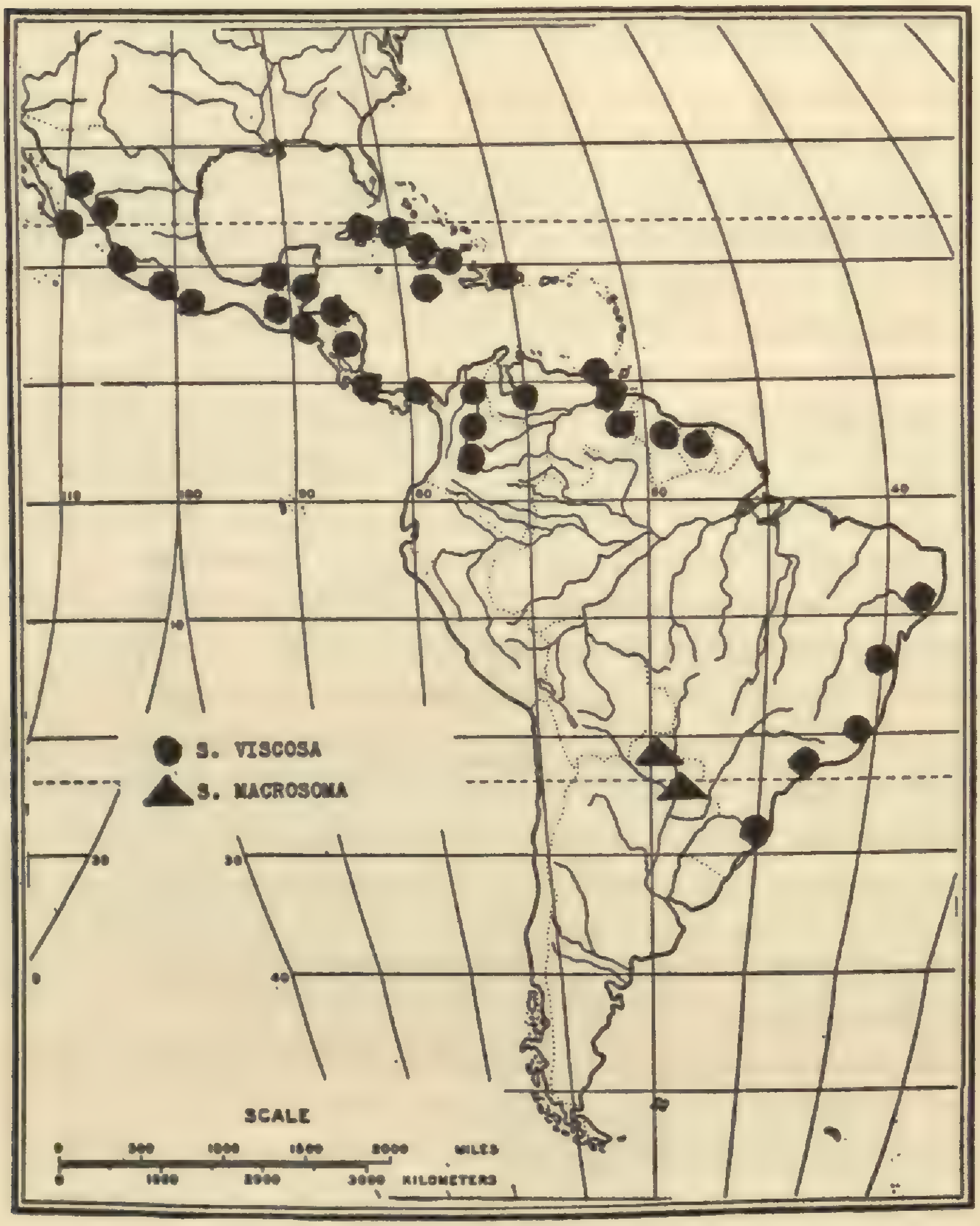

Fig. 8

the sheath 2.5–3.5 mm. long, 4.0 mm. broad, with scattered bristles and about 9 nerves, the teeth 3.5–4.0 mm. long; outer bracteole 3.0–3.5 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 1.0–2.5 mm. long, ciliate at the apex. Calyx tube 2.5–3.5 mm. long, the lobes 2–3 mm. long and ciliate. Standard suborbiculate, 4–5 mm. long; wings 3.5–4.5 mm. long, obovate, auriculate at the base and shortly appendaged within; keel petals 3–4 mm. long, subrostrate. Loment 2.0–2.5 mm. broad, weakly nerved; only the upper articulation of the loment fertile, 3.5–5.0 mm. long, glabrous except for some short hairs on the margin near the summit; beak strongly uncinate to nearly coiled, 1.5–2.5 mm. long, less than half as long as the upper articulation.

The type was distributed as S. *guyanensis* although Morong noted on the collection label that it was not quite like other specimens of S. *guyanensis* which he had collected. Hassler named this species as a form of S. *montevidensis*.

PARAGUAY: ASUNCIÓN: exact locality unknown, *Morong 255* (US, MO, GH, NY). WITHOUT PRECISE LOCALITY: *Hassler 7606* (GH, NY).

22. STYLOSANTHES VISCOSA Sw. in Prod. Veg. Ind. Occ. 108. 1788, ex char.

Hedysarum hamatum β L. Syst. Nat. 10:1170. 1759, ex char.
Stylosanthes glutinosa HBK. Nov. Gen. et Sp. 6:507. 1823, ex char.
Stylosanthes viscosa β *acutifolia* Benth. in Mart. Fl. Bras. 15^1:91. 1859, ex char.
Stylosanthes viscosa f. *typica* Hass. in Fedde, Rep. Sp. Nov. 16:220. 1919, ex char.
Stylosanthes prostrata M. E. Jones, in Contrib. West. Bot. 15:135. 1929. (T: *Jones 24002*!)

Stems ascending and spreading or prostrate and matted, much branched, to 1 m. long, densely pubescent with short viscid hairs. Leaflets to 25 mm. long, 5 mm. broad, usually much smaller, acute or obtuse, punctate beneath, shortly hairy or hispidulous, with 2–4 pairs of conspicuous veins; petioles 2.5–5.0 mm. long, hispidulous, viscid, the rhachis 1–2 mm. long; sheath of the stipules 3.5–5.5 mm. long, 1–2 mm. longer than the teeth, hispidulous and viscid on the back, 3- to 5-nerved. Spikes small, crowded, ovoid, 2-to 5-flowered; outer bracts usually trifoliolate, inner unifoliolate, the sheath equaling or slightly exceeding the teeth, hispidulous and viscid on the back, 5- to 7-nerved; outer bracteole 1, 2.5–3.0 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2.5–3.0 mm. long, ciliate at the apex. Calyx tube 3–7 mm. long, glabrous to puberulent. Standard suborbiculate, 4–7 mm. long; wings 4–5 mm. long, auriculate, spurred within at the base; keel petals 3–4 mm. long, falcate. Loment to 2.5 mm. broad; only the upper articulation of the loment fertile, 2–4 mm. long, shortly hairy, reticulate-nerved; beak short, less than half as long as the upper articulation, usually about one-third to one-fourth as long, shortly hairy, strongly uncinate, often coiled.

Most specimens possess subacute or obtuse leaflets 5–15 mm. long. Some have acuminate leaflets 15–25 mm. long, and these have been segregated as var. *acutifolia.* This variation occurs throughout the entire range of the species, however, although most of the specimens with longer leaflets are found in the southern part of the range.

Stylosanthes prostrata of Baja California is merely a heavily viscid, prostrate form of *S. viscosa.*

Stylosanthes viscosa has been reported several times as an adventive along the western coast of Africa.

CUBA: CAMAGÜEY: Camagüey to Santa Ana, *Britton 1960* (NY, US); south of Sierra Cubitas, *Shafer 505* (NY). HABANA: Guanabacoa, *Baker 2930* (NY); Gran Sierra, *Clemente 2078* (NY); Loma de las Yatas, *Ekman 574* (US); Loma de la Juta, *Wilson & León 11643* (NY, US); exact locality unknown, *Taber 1930* (NY). LAS VILLAS: Santa Clara, vicinity of Sancti Spiritus, *Shafer 12120* (GH, NY, MO, US, F); 12 km. east of Cascajal, *Howard 5578* (GH), *85534* (GH, NY); Cienfuegos, *Combs 407* (GH, US, NY, MO, F); La Magdalena, Cayamas, *Baker 2503* (NY, US); Manacas, *Jack 8713* (NY). ORIENTE: El Cobre, *Britton, Cowell & Shafer 12866* (NY, MO, US); Guantanamo Bay, *Britton 1960* (NY, US); exact locality unknown, *Wright 122* (GH, NY, MO). WITHOUT PRECISE LOCALITY: *Linden s. n.* (NY).

DOMINICAN REPUBLIC: SANTIAGO: El Rubio, *Jimenez 1058* (US). SANTO DOMINGO: Monte Cristi, *Ekman 12633* (US).

JAMAICA: Two-Mile-Wood, St. Catherine, *Harris 12406* (GH, NY, MO, US, F); Lititz savana, *Harris 12899* (GH, NY, MO, US, F); Abbey Green, *Orcutt 2869* (US); Kingston, *Hansen 1897* (NY); Spring Hill, Portland, *Harris 6630* (NY, US, F).

El Salvador: near Chalchuapa, *Calderón 1008* (US, GH).

Guatemala: jalapa: between Monjos and Jalapa, *Steyermark 32209* (F). jutiapa: Cerro Colorado, *Standley 76183* (F).

Honduras: comayagua: vicinity of Comayagua, *Standley & Chacón 5385, 5403* (F); Siguatepeque, *Standley 5627S* (F, US). el cayo: exact locality unknown, *Gentle 2245* (GH, F). morazán: Las Mesas, *Swallen 10793* (US); west of Chaquito, near Río Yeguare, *Standley 22948* (US); San Antonio, *Rodríguez 667* (F). el paraíso: Quebrada de Dantas, *Standley, Williams & Molina 1289* (F); Yuscarán, *Molina 1658* (F).

Mexico: baja california: San José del Cabo, *Jones 24002* (GH, NY, MO, US, F), *27236* (GH, US); Todos Santos, *Jones 24769* (MO, NY, F); Cape San Lucas, *Rose 16364* (NY, US). chiapas: Hacienda Monserrate, *Purpus 9126* (US); between Tapana, Oaxaca, and Tomala, *Nelson 2945* (US), *2950* (US). colima: east side of Manzanillo Bay, *Ferris 6199* (US). guerrero: 4 miles north of Acapulco, *Barkley, Rowell & Westlund 30* (F); Acapulco, *Palmer 10* (GH, MO). jalisco: San Sebastian, northeast of Hacienda del Cura, *Mexia 1373* (GH, MO). sinaloa: Río Florido, *Dehesa 1525* (US); Santa Lucia Concordia, *Dehesa 1632* (US). sonora: Alamos, *Rose, Standley & Russell 12693* (GH, US, F); Alamos, Río Puerte, *Gentry 2934* (GH, MO, US, F). tabasco: Achotal, Balancán, *Matuda 3041* (F, NY), *3047* (NY, F). zacatecas: near San Juan Capistrano, *Rose 2467* (GH, US).

Nicaragua: Volcán El Viejo, *Oersted 4740* (F).

Panama: panamá: vicinity of San Carlos, *Allen 1143* (GH, US, MO, NY).

Bolivia: cochabamba: Ayopaya, Sailopata, *Cardena 3186* (F). without precise locality: São Yungas, *Büchtien 210* (US); Urupana, *White 942* (NY).

Brazil: baía: Mt. Peludo, *Curran 391* (GH, US, F); Machado Portela, *Rose & Russell 19956* (US); Ilha de Itaparica, *Pires 3421* (NY); Busca Vida, *Bondar 2598* (F). distrito federal: Ipanema, *Barreto 5600* (F). minas geraes: Lassance, Pirapora, *Cochran s. n.* (US); Tejuco, *Vauthier 163* (GH); Ilheos, *Riedel 211-212* (GH, US). pernambuco: Prazeres, *Pickel 980* (GH, US, NY); Tapera, *Pickel 186* (F). rio de janeiro: near Rio de Janeiro, *Burchell 4109* (GH), *1174* (GH, NY); Copacabana, *Glaziou 5817* (NY). santa catarina: Laguna, *Reitz & Klein 4677* (US). são paulo: Campiña, *Krug & Zagatto 2191* (US); Butantan, *Gehrt 25239* (NY).

British Guiana: Berbice (or Demerara) Co., *Abraham 89* (NY); exact locality unknown, *Schomburgk 178* (US, NY).

Colombia: cundinamarca: Melgar, *Pennell 3608* (GH, US, NY, F). huila: east of Neiva, *Rusby & Pennell 1083* (GH, US, NY), *1042* (NY). magdalena: Rincón Hondo, *Allen 405* (MO). santander: Lebrija, *Molina 376* (US). tolima: Doima, *Haught 2444* (MO, US, F, NY); Honda, *Pennell 3608* (GH, US, NY, MO).

Paraguay: la cordillera: Ypacaray, *Hassler 11576* (GH, US, NY, MO). without precise locality: between Río Apa and Río Aquidaban-mí, *Fiebrig 4384-4082* (GH, US).

Surinam: Zanderij Island, *Maguire & Stahel 23733* (NY, US, F); Sectie Oeest, *Stahel & Gonggrüp 523* (US); Corantijn River, *Rombouts 166* (NY).

Venezuela: bolívar: Island of Margarita, Pt. Mosquito, *Johnston 249* (GH); between Ciudad Bolívar and El Cristo, *Killip 37234* (US); between Upata and Río Caroní, *Steyermark 57563* (MO, F). nueva esparta: Cocke Island, *Johnston 6* (US, GH). trujillo: Loma de Moron, near Valera, *Pittier 10721* (GH, US, NY).

23. Stylosanthes **figueroae** Mohlenbrock, sp. nov.

Herba humistrata vel suberecta basi ramosissima ad 20 cm. longa caulibus glabris vel puberulis. Foliola elliptico-ovata puberula nervis 3–5-gemmatis; foliolo terminali ad 10 mm. longo 5 mm. lato; foliolis lateralibus ad 10 mm. longis; petiolo 1–3 mm. longo glabro vel puberulo; rhachide 0.5–1.5 mm. longa; stipulae striatae vagina 3–7 mm. longa glabra vel puberula processibus subulatis mucronatis 3–5 mm. longis. Spicae parvae oblongoideae floribus 2–7; bracteis plerumque uni-

foliolatis stipuliformibus vagina puberula 3–6 mm. longa nervis 3–7; bracteola exteriore 1, 2.5–4.0 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.0–3.5 mm. longa apice ciliata. Calycis tubus 3.5–5.5 mm. longus glaber lobis 1.5–2.5 mm. longis. Corolla lutea; vexillo suborbiculato 4.0–5.5 mm. longo; alis falcatis 3.5–4.5 mm. longis; carina 3.5–4.5 mm. longa. Lomentum pubescens circa 2 mm. latum reticulatum; articulo superiore 2.5–3.0 mm. longo puberulo; articulo inferiore abortivo; rostro 2.0–2.5 mm. longo uncinato puberulo.

Stylosanthes figueroae is distinguished from other members of its section by the pubescent loments with only one fertile articulation. It most nearly resembles *S. humilis* from which it differs in having the beak of the loment one-half to two-thirds the length of the upper articulation, rather than two to six times as long.

This species is known only from the vicinity of Cali, Colombia.

COLOMBIA: CAUCA: Cali, *Figueroa 897* (US, HOLOTYPE); Cauca, *Triana s. n.* (NY).

24. STYLOSANTHES MONTEVIDENSIS Vog. in Linnaea 12:67. 1838. (T: *Sellow s.n.*!)

Stylosanthes juncea Micheli, in Mem. Soc. Phys. Genève 28:7. 1883, ex char.
Stylosanthes juncea var. *setosa* Chod. & Hass. in Bull. Herb. Boiss., ser. 2, 4:884. 1904, ex char.
Stylosanthes montevidensis var. *juncea* (Mich.) Hass. in Fedde, Rep. Sp. Nov. 16:223. 1919.
Stylosanthes montevidensis f. *glabrata* Hass. in Fedde, loc. cit. 1919. (T: *Hassler 2709*!)
Stylosanthes montevidensis f. *setosa* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes montevidensis f. *typica* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes linearis Blake, in Jour. Wash. Acad. Sci. 14:287. 1924. (T: *Jörgensen 2693*!)
Stylosanthes gracilis var. *rostrata* Burkart, in Darwiniana 3:251. 1939, ex char.
Stylosanthes montevidensis var. *heterophylla* Burk. loc. cit. 260. 1939, ex char. (T: *Dusén s. n.*)
Astyposanthes montevidensis (Vog.) Herter, in Rev. Sudamer. Bot. 7:210. 1943.

Stems usually erect, to 1 m. tall, slender to robust, simple or often sparsely branched, glabrous to puberulent above or rarely throughout, usually with scattered long bristles. Leaflets lanceolate to linear, acute and mucronulate, glabrous to shortly hairy or occasionally with bristles along the costa beneath, with 2–4 pairs of conspicuous veins forming a submarginal nerve; terminal leaflet to 4 cm. long and 3 mm. broad, the lateral ones to 3 cm. long and 2.5 mm. broad; petioles 2.5–7.0 mm. long, glabrous, hispidulous, or short-bristly, the rhachis about 1 mm. long; sheath of the stipules 5–11 mm. long, sparsely bristly or densely short-hairy or rarely glabrous and with 13–21 often conspicuous nerves, the subulate teeth 3.0–7.5 mm. long, averaging about 4 mm. shorter than the sheath. Spikes globose, very small and few-flowered to large and over 40-flowered; bracts unifoliolate, the leaflet 2–5 mm. long, the sheath 2.5–4.5 mm. long, 2.5–5.0 mm. broad, ciliate along the margins or occasionally with a few bristles near the apex, usually 7-nerved, the teeth 1–4 mm. long; outer bracteole 1, 3–4 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2–3 mm. long, often bifid, ciliate at the apex. Calyx tube 2–5 mm. long, the lobes 2–3 mm. long. Standard suborbiculate, 4.0–6.5 mm. long; wings 3.5–5.0 mm. long, auriculate at the base; keel petals 3.5–4.5

mm. long, falcate. Loment 2–3 mm. broad, reticulate-nerved; only the upper articulation fertile, 3.0–5.5 mm. long, densely short hairy, at least near the apex; beak strongly uncinate, densely short hairy, 1.5–2.5 mm. long, one-half to one-third as long as the upper articulation.

The variability of the species is attested to by the many varieties and forms which have been proposed. Many of these are based on tenuous characters, and there is no line of demarcation separating any of them. Micheli proposed S. *juncea* as a new species on the basis of the stem usually 4 mm. or more in diameter as opposed to 2 mm. for S. *montevidensis*. Hassler divided the S. *montevidensis* complex into two forms of "typical" S. *montevidensis* and two forms of var. *juncea*, recognizing the latter as a variety, even though stating that it was merely a robust form.

Blake described S. *linearis* in § STYLOSANTHES because of the presence of an axis rudiment 0.3–0.8 mm. long. This character was not discovered in the present study of the type. Blake also noted the presence of 2 bractlets (= inner bracteoles), but there is actually only 1 deeply bifid inner bracteole.

The size of the inflorescence is exceedingly variable, specimens at one extreme having spikes 2- to 5-flowered while those at the other extreme have spikes over 40-flowered.

Stylosanthes montevidensis is recognized from other members of its section by the one fertile pubescent articulation with the circinate beak about one-half as long as the articulation.

A specimen collected by Calderón from El Salvador in all probability is adventive although the species does extend from Argentina to Colombia.

EL SALVADOR: near Chalchuapa, *Calderón 1051* (NY, US).

ARGENTINA: CHACO: Resistencia, Margarita Belen, *Aguilar 1163* (MO); Las Palmas, *Jörgensen 2693* (GH, US, MO). CÓRDOBA: Sierra Chico, *Lossen 173* (GH, MO, F). CORRIENTES: San Martín, La Cruz, *Ibarrola 1770* (US); Estancia, Santa Teresa, *Pedersen 111* (US); Empedrado, *Pedersen 908* (US). CRUZ ALTA: Campi Alegre, *Schreiter 4078* (F). JUJUY: Capital, Quebrada de Chañi, *Schreiter 11083* (GH). MISIONES: Candelaria, Garupa, *Bertoni 2382* (F); Apóstoles, *Clos 1911* (GH). SALTA: Guachipas, Alemania, *Venturi 9957* (GH, US, MO). SANTA FÉ: Reconquista F.C.S.F., *Burkart 5883* (GH). TUCUMÁN: Burruyaco, *Venturi 2616* (GH, US) Las Cejas, *Venturi 2117* (US); Campa Alegra, *Venturi s. n.* (US). WITHOUT PRECISE LOCALITY: Cafi, Cancillo, *Venturi 5992* (US); La Granja, *Ekman 1743* (NY, US, MO).

BOLIVIA: LA PAZ: La Paz, *Bang s. n.* (US). SANTA CRUZ: Sara, Buena Vista, *Steinbach 6922* (GH, MO, F), *5243* (GH), *3219* (F), *6614* (F).

BRAZIL: PARANÁ: Serrinka, *Dusén 16261* (GH), *13718* (NY, US). RIO GRANDE DO SUL: Porto Alegro, *Malme 726* (F). SANTA CATARINA: Sombrio, *Collector Unknown C1397* (GH). SÃO PAULO: Capital, *Pickel 5499* (US). WITHOUT PRECISE LOCALITY: Turnig, *Dusén 9147* (US).

COLOMBIA: META: San Martín, *Dryander 3038* (US).

PARAGUAY: CENTRAL: Caballero, *Morong 399* (NY, US, MO). PRESIDENTE HAYES: Santa Elisa, *Hassler 2709* (GH, MO). WITHOUT PRECISE LOCALITY: Estancia Primera, *Jörgensen 4817* (NY, US, MO, F); Coro de Altos, *Hassler 1798* (NY), *1799* (NY).

URUGUAY: CANALONES: Atlantida, *Rosengurtt B2830* (NY). CERRO LARGO: Río Negro, Palleros, *Rosengurtt B79* (NY). COLÓNIA: Arroyo de Pintos, Artilleros, near Puerto Platero, *Bartlett 21194* (GH). CONCEPCIÓN: Guinta del Colegio, *Lorentz s. n.* (US). SALTO: San Antonio, *Osten 5375* (US); San Antonio, *Rosengurtt B1070* (GH, F).

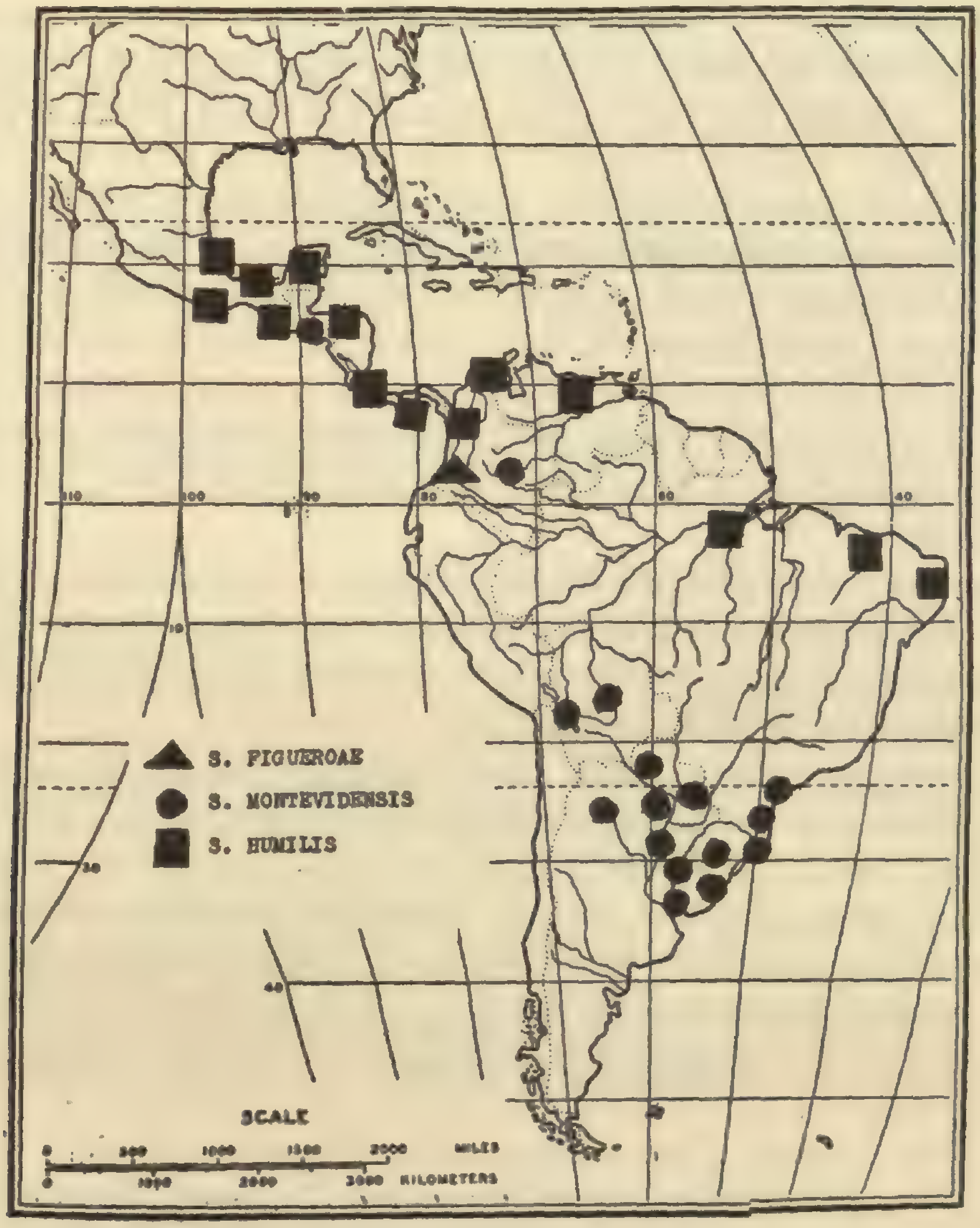

Fig. 9

25. Stylosanthes humilis HBK. Nov. Gen. et Sp. 6:506. 1823, ex char.

Stylosanthes sundaica Taub. in Verh. Bot. Brand. 32:21. 1890, ex char.
Astyposanthes humilis (HBK.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems usually ascending or sometimes prostrate, herbaceous to subligneous at the base, to 0.5 m. tall, branched, usually with short white hairs along one side of the stem, often with scattered short bristles, rarely nearly glabrous except near the base, the pubescence usually more dense immediately beneath each node. Leaflets lanceolate or sometimes elliptic, often mucronate, acute, short bristly-ciliate to nearly glabrous, with 3–4 pairs or usually conspicuous veins; terminal leaflet to 15 mm. long (rarely to 30 mm. long) and 3.5 mm. broad, the lateral ones to 11.5 mm. long and 3.0 mm. broad; petioles 2.5–5.0 mm. long, shortly hairy and often with scattered bristles, the rhachis 1–2 mm. long; sheath of the stipules 3–5 mm. long,

short-bristly and with 5–7 nerves, the teeth 2.5–3.5 mm. long, averaging about 1 mm. shorter than the sheath. Spikes short, ovoid, crowded, 3- to 4-flowered; bracts 1- to 3-foliolate, the sheath 2.5–4.5 mm. broad, nearly always bristly, rarely only ciliate, with 5–9 nerves, the teeth 2–3 mm. long; outer bracteole 2.5–3.0 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2.0–2.5 mm. long, ciliate at the apex. Calyx tube 4–5 mm. long, the acute lobes 1.5 mm. long. Standard suborbiculate, spurred within at the base, 3–4 mm. long; wings 3–4 mm. long, clawed and auriculate at the base; keel petals 3.0–3.5 mm. long, falcate. Loment 1.5–2.5 mm. broad, reticulate-nerved; only the upper articulation fertile, 1.5–2.5 (–4.0) mm. long, usually only puberulent, rarely pilose; beak strongly uncinate to coiled, 1.5–3.5 (–5.5) mm. long, equaling to greatly surpassing the upper articulation.

Stylosanthes humilis is variable in size and shape of the leaflets and in size of the loments. Most specimens have leaflets less than 1 cm. long; others, to 3 cm. long. The size of the loment including the beak ranges from 3.5 to 9.0 mm. long. These differences are not correlated geographically.

The species ranges from central Mexico through Guatemala and Panama to Colombia, Venezuela, and Brazil; also occurs in the Antilles and is adventive in Malaysia and Australia. Specimens from Malaysia described by Taubert as *S. sundaica* are actually *S. humilis*. Taubert included *S. sundaica* in § STYLOSANTHES but with the axis rudiment "most caducous." In the specimens examined, no trace of an axis rudiment could be found.

CUBA: CAMAGÜEY: La Gloria, *Shafer 239* (NY). LAS VILLAS: Lomas de Bañao, *Luna 730* (NY).

EL SALVADOR: vicinity of San Salvador, *Standley 19399* (GH, US, NY).

GUATEMALA: CHIQUIMULA: between Zacapa and Chiquimula, *Standley 73693* (F); near Chiquimula, *Standley 73862* (F); north of Quezaltepeque, *Steyermark 31372* (US, F). ESCUINTLA: Río Guacalate, *Standley 58237* (NY, F). GUATEMALA: near Guatemala and Fiscal, *Standley 59788* (F). JALAPA: vicinity of Jalapa, *Standley 76411* (F). JUTIAPA: between Jutiapa and Plan de Urrutia, *Standley 75455, 74910, 75652* (F); between Agua Blanca and Amatillo, *Steyermark 30457* (F), *30450* (F). QUICHÉ: exact locality unknown, *Aguilar 1407* (F). SANTA ROSA: plains of Llano Entero, southeast of Chiquimulilla, *Standley 78796* (F); south of Guezacapan, *Standley 79431* (F); near Cuilapa, *Standley 77942* (F); Chupadero, *Heyde & Lux 4162* (GH, US). ZACAPA: vicinity of Zacapa, *Standley 74588, 73589* (F); between La Fragna and Estanzuela, *Steyermark 29126* (F).

HONDURAS: MORAZÁN: Río Yeguare, *Williams & Molina 16967* (GH, US, F); Agua Amarilla, *Williams & Molina 11027* (F); El Zamorano, *Rodríguez 1257, 2163* (F). EL PARAÍSO: exact locality unknown, *Standley 13600* (NY, US, F). YORO: near Progreso, *Standley 55048* (US, F).

MEXICO: CHIAPAS: Jalisco, *Purpus 9138* (US). COLIMA: Colima, *Palmer 108* (US). GUERRERO: Cutzamala, Cayuca, *Hinton 6985* (NY, US, F); Acapulco, *Palmer 25* (GH, US, NY, MO, F). JALISCO: Tecoman, *Orcutt 4447* (MO, GH, F); Barranca de Portillo, *Barnes & Land 240* (GH, US, F). MÉXICO: Temascaltepec, Tejupilco, *Hinton 1932* (US), *1931* (GH), *4767* (GH, US). MICHOACÁN: Apatzingán, Aguililla, *Hinton 5289* (US, GH, NY). OAXACA: San Gerónimo, *Mell 2117* (NY). VERA CRUZ: Acasonica, *Purpus 8894* (GH, US, MO); Zacuapán, *Purpus 2331* (GH, US, NY, MO, F); Minatitlán, *J. G. Smith 408* (MO).

PANAMA: CANAL ZONE: Corozal, *Standley 27403* (US); between Fort Clayton and Corozal, *Standley 29191* (US). COCLÉ: Aguadulce, *Pittier 4837* (US), *4983* (GH, NY, US). PANAMÁ: Las Sabanas, *Standley 41178* (US); near Panamá, *Standley 26794, 27730* (US); near Punta Paitilla, *Standley 26293* (US); between Panamá and Chêpo, *Dodge, Hunter, Steyermark & Allen 16700* (MO). VERAGUAS: west of Soná, *Allen 1054* (GH, US, MO).

BRAZIL: BAÍA: (data not legible) (MO). CEARÁ: Acude São Bento, Maranguape, *Drouet 2194* (GH, NY, MO, US, F). PARÁ: Boim, Rio Tapajoz, *Kuhlmann 18223* (US). PERNAMBUCO: Tapera, *Pickel 3036* (GH, US, F). RIO GRANDE DO NORTE: Angicos, *Swallen 4737* (US).

COLOMBIA: ANTIOQUIA: exact locality unknown, *Gutierrez, Klevens & Barkley 1463* (US).

VENEZUELA: GUARÍCO: between La Encrucijada and Misión Abajo, *Pittier 14925* (US); Mesa de El Sombrero, *Pittier 12489* (MO). MÉRIDA: near Tovar, *Fendler 1793* (GH, MO). TRUJILLO: Dividine, *Pittier 10823* (US). ZULIA: Maracaibo, *Pittier 10698* (NY, GH, US).

AUSTRALIA: QUEENSLAND: Townsville, *White 8818* (NY, US).

MALAYSIA: BALI: Tedjazolla, *deVoogd 2061* (GH). NOESA PENIDA: Sampelan near Tanglad, *deVoogd 2397* (GH).

JAVA: *Horsfield 91* (GH).

EXCLUDED OR DUBIOUS SPECIES

Stylosanthes rigida Spreng. Syst. 3:310. 1826. This species is described by a single phrase which could well apply to a number of species of *Stylosanthes*.

Stylosanthes tenuifolia G. Don, Gen. Syst. 2:281. 1832. Don distinguishes this species, which is known from the "Isle of Maranham, Brazil," by its narrow leaflets. While this likely applies to *S. angustifolia*, it could apply to narrow-leaflet forms of *S. guyanensis*.

Stylosanthes suborbiculata Chiov. Ann. di Bot. 13:381. 1915. The type for this species (*Paoli 239*), collected in 1913 in Somaliland, has not been seen and is therefore excluded from the systematic treatment. Chiovenda describes it as without an axis rudiment which distinguishes it from all other African species of *Stylosanthes* except *S. viscosa* which is adventive along the western coast of Africa. A photograph of *S. suborbiculata* may be found in Result. Sc. Miss. Stefan.-Paoli Somal. Ital. *t. 8* (1916) but this is of little value in determining the exact status of the species.

Stylosanthes rupestris Stuck. ex Seckt, Rev. Univ. Nac. Córdoba 17^{3-4}:145. 1930. This is a *nomen nudum* with only the location given by the author—Sierra (Malaguena), Argentina.

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Italicized numbers refer to collectors' numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the numbers assigned to the species in this monograph.

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